

EFFECT OF WIND ON THE  
TRANSPIRATION OF YOUNG TREES

by

Michael Dixon, B.Sc., M.Sc.

Ph.D.

University of Edinburgh

1982



## TABLE OF CONTENTS

<u>DECLARATION</u>	v
<u>ACKNOWLEDGEMENTS</u>	vi
<u>LIST OF SYMBOLS</u>	vii
<u>ABSTRACT</u>	ix
<u>CHAPTER 1.</u> Introduction	1
MATERIALS AND METHODS	
<u>CHAPTER 2.</u> Measurement of Transpiration	12
2.1 Plant Material and Experimental Conditions	13
2.1.1 The Wind Tunnel	15
2.2 Temperature Sensing on Leaves	18
<u>CHAPTER 3.</u> Measurement of Aerodynamic Resistance/ Conductance	21
3.1 Technical Evaluation	25
3.1.1 Stomatal Component of Mass Transfer ( $r_s$ or $g_s$ )	25
3.1.2 Aerodynamic Component of Mass Transfer ( $r_a^w$ or $g_a^w$ )	25
3.1.3 Aerodynamic Component of Heat Transfer ( $r_a^h$ or $g_a^h$ )	28
3.2 The Cooling Curve Technique	32
<u>CHAPTER 4.</u> Measurement of Components of Water Potential	40
4.1 Technical Objective	40
4.1.1 Pressure Bomb Technique	40
4.1.2 Impedance Technique	41
4.1.3 Thermocouple Psychrometry	45
4.1.4 Other Techniques	47

4.2	Design and Construction of Thermocouple Psychrometer	49
4.2.1	Design	49
4.2.2	Thermocouples for Psychrometer Chambers	52
4.2.3	Calibration	56
4.3	Water Uptake by Some Chamber Materials	59

## RESULTS AND DISCUSSION

<u>CHAPTER 5.</u>	Experimental Determination of Heat Transfer	60
5.1	Effect of Leaf Form	61
5.2	Effect of Turbulence	65
5.3	Effect of Leaf Proximity	68
5.4	Comparison with Boundary Layer Theory	70
5.5	Discussion	76
<u>CHAPTER 6.</u>	The Effect of Wind on Transpiration	82
6.1	A Note on Resistances versus Conductances	83
6.2	Calculated Rates of Transpiration	84
6.3	Observed Rates of Transpiration	88
6.3.1	Observed Stomatal Resistances ( $r_s$ )	88
6.3.2	Observed Rates of Night-time Transpiration	95
6.4	Components of Water Potential	97
6.5	Discussion	99
6.5.1	Wind and Transpiration	99
6.5.2	Evaluation of Experimental Conditions	104
6.5.3	Sensitivity Analysis of the Penman-Monteith Equation	106
6.5.4	Reconsideration of Errors in Net Radiation	109
6.5.5	Errors in Other Parameters	111

6.5.6	Aerodynamic Resistance	113
6.5.7	Water Relations	114
<u>CHAPTER 7.</u>	Conclusions	120
<u>BIBLIOGRAPHY</u>		124
<u>APPENDIX A</u>	Thermocouple Output Amplifier	140
<u>APPENDIX B</u>	Water Uptake by Some Chamber Materials	141
<u>APPENDIX C</u>	Fortran Program "PENTEITH"	162
<u>APPENDIX D</u>	Radiation Environment of the Wind Tunnel	163



### DECLARATION

This thesis has been composed by myself  
from the results of my own work except  
where acknowledged to the contrary.

## ACKNOWLEDGEMENTS

The work described in this thesis was carried out in the Department of Forestry and Natural Resources, University of Edinburgh, during the tenure of two Natural Environment Research Council Research Grants.

My thanks are due to the following:

Dr. John Grace, my supervisor, for his advice and encouragement.

Mr. Alec Harrower and Mr. David Mackenzie for technical assistance and advice in the workshop.

Mr. Robert Astles for maintenance of glasshouse stocks.

Mr. James Follan for designing some of the electronic circuits.

Mr. Jeremy Landless for wind tunnel and growth room maintenance.

My colleagues, in this department and others, for contributing invaluable discussion and advice throughout the study.

And Kath.

## LIST OF SYMBOLS

A	total energy available for the exchanges of latent and sensible heat.
$A_p$	projected surface area.
b	specific heat of brass.
C	flux density of sensible heat in air.
$C_L$	specific heat of leaf tissue.
$C_p$	specific heat of air at constant pressure.
D	diffusion coefficient of water vapour in air.
d	characteristic dimension.
E	flux density of water vapour in air.
$e_a$	water vapour pressure in the ambient air.
$e_o$	water vapour pressure at the leaf surface.
$e_s(T_L)$	saturation vapour pressure at leaf temperature.
F	flux of a diffusing species.
$g_a$	aerodynamic conductance, denoted by superscript as to diffusing species.
$g_s$	stomatal conductance.
$h_c$	heat transfer coefficient.
L	total surface area.
m	slope of the plot of $\ln \Delta T$ against time.
R	flux of all-wave radiation into ( $R_{in}$ ) or out of ( $R_{out}$ ) the leaf.
$R_n$	net radiation
$r_a$	aerodynamic resistance, denoted by superscript as to diffusing species.

$r_s$	stomatal resistance.
$\Delta S$	change in stored energy.
$s$	slope of the saturation vapour pressure versus temperature curve for water at a given temperature.
SVPD	saturation vapour pressure deficit.
$T$	temperature, denoted by subscript.
$t$	time.
$u$	wind speed.
VPD	vapour pressure difference between leaf and air.
$w$	mass of the brass leaf.
$Z$	impedance.

#### GREEK LETTERS

$\kappa$	thermal diffusivity of dry air.
$X$	concentration of diffusing species, denoted by subscript.
$\lambda$	latent heat of vaporisation of water.
$\Pi$	osmotic potential.
$P$	turgor potential.
$\nu$	kinematic viscosity of dry air.
$T$	matric potential.
$\gamma$	psychrometric constant.
$\pi$	pi.
$\rho$	density of air.
$\Psi$	total water potential.

## ABSTRACT

The effects of wind on the transpiration rates of five plant species were studied in a controlled environment wind tunnel. When due consideration was given to the geometry of radiation fluxes in the wind tunnel, the average transpiration rates of the species tested followed closely those calculated using the Penman-Monteith equation, which predicts, in many conditions, a decrease in transpiration with increasing wind speed.

Aerodynamic resistance to heat transfer was estimated from cooling curves of brass leaf replicas placed in the canopy of the test species. Precise differential temperature measurements were made with a thermocouple output amplifier.

Heat exchange from brass leaf replicas was slightly enhanced with the addition of ripples or serrations to the leaf margin. Power spectrum analysis of the air flow in the boundary layers of these leaves showed that turbulent conditions prevailed, even at low Reynolds numbers, and low frequency turbulence (especially 200-500 Hz) correlated best with the observed increase in conductance.

A study into the water uptake properties of various materials used in the construction of thermocouple psychrometer chambers was carried out. It was found

that, of the materials tested, chromium plated brass and fluorocarbon rubber (e.g. Viton) were best suited for this purpose. These materials were used in the construction of a thermocouple psychrometer unit capable of equilibrating three samples at once. Technical refinements in thermocouple welding facilitated routine production of thermocouple junctions for psychrometer chambers.

Increasing wind tended to decrease total water potential and osmotic potential in Pinus sylvestris L. Turgor potential remained relatively constant suggesting a degree of osmotic adjustment.

## CHAPTER 1. Introduction

"Although considerable attention has been given to the influence of wind on transpiration, the results that have been obtained are very conflicting."

(Martin and Clements, 1935)

Almost half a century later this view still prevails, as shown by recent reviews of the subject (e.g. Grace, 1977).

It has been implied or stated in the ecological literature that high winds lead to greater rates of transpiration and hence to greater water stress (Daubenmire, 1959). This is supposed to account for various phenomena including the wind shaping of trees and the agricultural benefit of shelter. However, several authors, using the Penman-Monteith equation or an equivalent approach, have refuted this view (Gates and Papian, 1971; Grace, 1977; Monteith, 1965), and at least one author has shown experimentally that wind has little or no effect on transpiration under many ordinary conditions (Yamaoka, 1958). On the other hand there are reports which suggest that the effect of wind on plants is modified by stomatal behavior; that stomata may shut in response to the shock of wind treatment (Martin and Clements, 1935; Satoo, 1962; Tranquillini, 1969; Caldwell, 1970), or even open more widely (Grace, 1974). Some authors

have shown that wind causes stomatal or cuticular damage which could lead to greater rates of water loss (Grace, 1974; MacKerron, 1976; Wilson, 1978).

The research reported in this thesis was conceived as a study of the effects of wind on the transpiration of selected plant species, especially how these effects were influenced by certain physical and physiological parameters. Emphasis was placed on the development and evaluation of techniques used to estimate variables in this field and which hitherto have received insufficient attention.

A primary objective of this study was to test one of the predictions of the Penman-Monteith equation (Penman, 1948; Monteith, 1965) that, in many cases, an increase in wind speed results in a decrease in transpiration. The application of this model of evaporation from plant surfaces has received much attention in the literature (Thom, 1975; Campbell 1977; Jarvis, 1981). The following derivation of the Penman-Monteith equation is after Thom (1975) with some embellishments from Jarvis (1981). This model is potentially very valuable to plant scientists as it allows transpiration rates to be calculated from a knowledge of only a few parameters, all of which ought to be measurable with standard techniques.

The necessary component relationships of the Penman-Monteith equation comprise the following:



the energy balance relationship:

$$A = R_{in} - R_{out} - \Delta S = \lambda E + C \quad (1.1)$$

where  $A$  = total energy available for the exchanges  
of latent and sensible heat ( $W\ m^{-2}$ )  
 $R$  = flux of all wave radiation into ( $R_{in}$ )  
or out of ( $R_{out}$ ) the leaf ( $W\ m^{-2}$ )  
 $\Delta S$  = net change in stored energy including  
changes of sensible heat and metabolic  
energy in the biomass and changes in the  
sensible and latent heat content of the  
air ( $W\ m^{-2}$ )  
 $\lambda$  = latent heat of vaporisation of water  
( $J\ kg^{-1}$ )  
 $E$  = flux density of water vapour in air  
( $kg\ m^{-2}\ s^{-1}$ )  
 $C$  = flux density of sensible heat in air ( $W\ m^{-2}$ )

and the relationships evaluating the aerodynamic and  
physiological resistances to sensible and latent heat  
exchange between the plant and the atmosphere, namely:

the aerodynamic resistance to heat transfer ( $r_a^h$ ), which  
is proportional to the ratio of the leaf-air temperature  
difference (driving force) and the flux of sensible heat,  
and which is fundamentally determined by the properties

of the boundary layer over the leaf:

$$r_a^h = \rho C_p \frac{(T_L - T_a)}{C} \quad (1.2)$$

where  $\rho$  = density of air ( $\text{kg m}^{-3}$ )  
 $C_p$  = specific heat of air at constant  
pressure ( $\text{J kg}^{-1} \text{ } ^\circ\text{C}^{-1}$ )  
 $T_L$  = leaf temperature ( $^\circ\text{C}$ )  
 $T_a$  = air temperature ( $^\circ\text{C}$ )

Similarly, the aerodynamic resistance to water vapour exchange ( $r_a^w$ ) is proportional to the ratio of the leaf-air vapour pressure difference and the flux of latent heat:

$$r_a^w = \frac{\rho C_p}{\gamma} \cdot \frac{(e_o - e_a)}{\lambda E} \quad (1.3)$$

where  $e_o$  = vapour pressure at the leaf surface (mb)  
 $e_a$  = vapour pressure in the ambient air (mb)  
 $\gamma$  = psychrometric constant ( $\text{mb } ^\circ\text{C}^{-1}$ )

The physiological or stomatal resistance is defined as:

$$r_s = \frac{\rho C_p}{\gamma} \cdot \frac{(e_s(T_L) - e_o)}{\lambda E} \quad (1.4)$$

where  $e_s(T_L)$  = vapour pressure in the sub-stomatal cavity (generally accepted to be the saturation vapour pressure at leaf temperature ( $T_L$ )). (mb)

The equation for  $\lambda E$  is obtained by combining these four relationships to eliminate the 'unknown' values of leaf temperature and leaf surface and sub-stomatal vapour pressures as follows:

$e_o$  is eliminated by the addition of equations (1.3) and (1.4) to give:

$$r_a^w + r_s = \frac{\rho C_p}{\gamma} \cdot \frac{(e_s(T_L) - e_a)}{\lambda E} \quad (1.5)$$

To eliminate the need to measure leaf temperature the following substitution must be made:

$$e_s(T_L) = e_s(T_a) + s(T_L - T_a) \quad (1.6)$$

where  $s$  = slope of the saturation vapour pressure versus temperature curve for water at the mean of  $T_L$  and  $T_a$  (or at  $T_a$  if  $T_L$  is unknown).

Note: A more detailed explanation of this substitution is given by Monteith (1965).

It is well worth noting that this substitution will not lead to serious error when  $T_a$  is low and

$(T_L - T_a)$  is small, as is often the case in temperate climates.

Equations (1.1) and (1.2) are then employed to replace the difference  $(T_L - T_a)$  by the product  $(A - \lambda E)r_a^h / \rho C_p$ . Subsequent substitution of equation (1.6) into equation (1.5) then permits the latter, with some algebraic manipulation, to be solved for  $\lambda E$ , in the form:

$$\lambda E = \frac{sA + \rho C_p (e_s(T_a) - e_a) / r_a^h}{s + \gamma(r_a^w + r_s) / r_a^h} \quad (1.7)$$

For daytime conditions, apart from dawn and dusk, the assumption is made that the stored energy term ( $\Delta S$ ) from equation (1.1) is small relative to the difference in net radiation flux ( $R_{in} - R_{out} = R_n$ , where  $R_n$  = net radiation to the leaf) and can often be neglected. This assumption is all the more valid in a controlled environment where ambient fluctuations in sensible and latent heat content are kept to a minimum. Hence, the available energy for latent and sensible heat exchange ( $A$ ) is essentially equal to the net radiation that the leaf absorbs.

Finally, a minor correction stemming from the differing diffusivities of heat and water vapour in air is considered. The resistance of the boundary layer is proportional to the (molecular diffusivity in air)<sup>2/3</sup>

of the diffusing species being considered (Thom, 1968). The diffusivities of heat and water vapour in air at 20 °C are 0.215 and 0.242 cm<sup>2</sup> s<sup>-1</sup> respectively (Monteith, 1973). Assuming that the pathway across the boundary layer is identical for both heat and water vapour,

$$\frac{r_a^h}{r_a^w} = \left( \frac{0.215}{0.242} \right)^{\frac{2}{3}} = 0.924 \quad (1.8)$$

For approximate purposes it can be assumed that  $r_a^h$  and  $r_a^w$  are equal. Otherwise it is acceptable to measure either of them, and infer the other from the above relationship. A further correction must be made in cases where the leaf is hypostomatous, as in such cases heat is lost from both sides of the lamina whilst water vapour is lost on one side only. Moreover, great care is required to ensure that radiation is expressed on the same basis (e.g. plan area of the leaf) as that of the resistances.

Inspection of equation (1.7) shows that evaporation ( $\lambda E$ ) essentially depends on the energy absorbed ( $A$ ), the saturation deficit of the atmosphere ( $e_s(T_a) - e_a$ ), the stomatal resistance ( $r_s$ ) and the aerodynamic resistance ( $r_a$ ). The latter is known to be a function of leaf size and wind speed. The form of equation (1.7) is such that the response of  $\lambda E$  to these variables is not clear from inspection, so that it is necessary to

set up the calculation with typical values in order to predict how each variable influences  $\lambda E$ . Moreover, the sensitivity of  $\lambda E$  to changes in the variables will depend on the particular combination of values chosen, and is unlikely to be linear.

The equation has been widely used in the analysis of evapo-transpiration from entire stands of vegetation. In such cases the vegetation is considered as a large horizontal surface characterised by  $r_s$  and  $r_a$ , and the net radiation can be conveniently measured above the vegetation using a Funk-type net radiometer. A small correction is usually made to allow for heat flux to the ground, usually utilizing soil heat flux plates. However, the equation is of universal application to any evaporating object including the wet bulbs of hygrometers, fruits and leaves. The main difficulty in its application to such structures is the problem of knowing how much energy is absorbed by the object. A spherical object, such as an apple, exchanges radiative energy with its surroundings in all directions. A small free-standing tree also exchanges energy in all directions, and its response is considerably affected by the distribution of leaf angle.

The primary experimental objective involved evaluation of all the environmental and physiological parameters controlling transpiration from young trees in a wind tunnel (refer to equation (1.7)). The experiment

was designed to change only one variable, that of wind speed (and hence  $r_a$ ). In addition, measurements of plant water status, in terms of total water potential and its components, turgor and osmotic potentials, were sought. It was thus intended to calculate the transpiration rate at a range of wind speeds from a knowledge of the main variables, and to observe the transpiration rate by weighing the plants in their pots over a period of time.

This approach to the testing of the prediction of the Penman-Monteith equation required great care in the evaluation and application of various techniques. In particular, it was felt that the aerodynamic resistance has been inadequately measured in the past as there are well known discrepancies in the literature (Grace, 1981; Monteith, 1981). Moreover, it was realised that measurements of leaf-air temperature differentials and plant water status, though not required in the Penman-Monteith equation, would greatly facilitate the interpretation of results and the exploration of their wider significance. Consequently, major efforts were made to develop techniques in these areas to a point where they could be used reliably and routinely in our laboratory.

Chapter 2 is concerned with the general experimental design and conditions adopted for the basic experiments on wind and water loss. Also, the problem of leaf

temperature measurement is examined since knowledge of this variable is critical to an estimate of the effect of wind on the driving force for transpiration.

Chapter 3 explores the variety of techniques employed in the past to measure aerodynamic resistance to diffusion of heat and water vapour. The choice of the cooling curve technique (Grace, et al, 1980) for the present investigation required the design and construction of an electronic thermocouple amplifier capable of resolving 0.01°C.

The measurement of the components of water potential is the subject of Chapter 4. The widely accepted 'pressure bomb' technique (Scholander and Hamel, 1965) and the less well known impedance technique (Dixon, et al, 1978) are explored. Finally, the thermocouple psychrometer (Spanner, 1951) is selected as the technique most suited to this application and a detailed program of research and development evolved, centered on this instrument. This resulted in the design and construction of a cheap and reliable thermocouple psychrometer which could be used in conjunction with the Wescor HR33T microvoltmeter or equivalent. Unfortunately, most of the species used in this study turned out to be unamenable to measurement of total water potential using this technique, a problem which could not have been foreseen at the start of the work. However, good data were obtained for Pinus sylvestris.



Chapter 5 describes the results of experimental investigation of the boundary layers of model leaves of assorted design. The techniques of hot-wire anemometry and power spectrum analysis provide an extremely detailed view of the diffusion path for heat and water vapour at the leaf surface. An attempt is made to extrapolate this knowledge to a consideration of the same processes in the real leaves used in the wind and transpiration experiments.

The measurements of transpiration in the five species used in this study, as well as concurrent estimates of the key environmental and physiological variables required to assess the effects of wind on transpiration, are presented in Chapter 6. These results are analysed and discussed along with previously published data. The Penman-Monteith equation is subjected to a sensitivity analysis to evaluate possible sources of error and relative magnitudes.

Finally, Chapter 7 outlines the experimental and technical findings of this research.

## MATERIALS AND METHODS

## CHAPTER 2. Measurement of Transpiration

The measurement of transpiration can be accomplished by a number of methods, the most straightforward of which is the gravimetric technique (periodic weighing of plants). The use of diffusion porometers, although often necessary in assessing transpiration from plants rooted naturally in the field, is indirect. The various types of diffusion porometer have in common several sources of error. These include temperature sensitivity, instability and hysteresis of the sensor, water adsorption properties of the construction materials and errors in calibration (Jarvis, 1981). Perhaps the biggest difficulty with modern null balance porometers is the assumption of isothermal conditions within the chamber (Parkinson and Day, 1980). Whereas this assumption may not lead to much error in the case of conifer needles, it is more likely to be important for broad-leaved species in which aerodynamic resistance is higher. Various methods involving measurement of water flow in the stem, such as the heat pulse technique (Edwards, 1981), are also difficult to calibrate. On the other hand, the gravimetric technique is a simple means of obtaining transpiration measurements which lent itself to this investigation, since all sample plants were individually potted and of convenient sizes for weighing.

## 2.1 Plant Material and Experimental Conditions

The sample species were chosen mainly on the basis of diversity in leaf morphology. The species were Rhododendron ponticum L., Pinus sylvestris L., Quercus robur L., Fagus sylvatica L., Sorbus aucuparia L. Plants were obtained as one plus ones and used in experiments within six to eighteen months. They were in rigid plastic pots with a volume of about 2050 cm<sup>3</sup> and the potting medium was U.C. Mix II(D) (Baker, 1957). To reduce environmental shock all sample plants were subjected to an acclimation period prior to each experiment. Depending on time of year this included 6-8 weeks in a greenhouse at 16 -20 °C followed by a further 4-6 weeks in a controlled environment growth chamber set at the experimental conditions.

The experimental conditions included a twelve hour photoperiod and an average ambient temperature of 20 °C. The relative humidity was set to 70-75% and monitored with a dew point hygrometer (Model 880, Cambridge Systems, Inc.) and an Assmann hygrometer (Casella and Co. Ltd., London) in conjunction with hygrometric tables (Meteorological Office, 1964). The average net radiation was 200-300 w m<sup>-2</sup> and was recorded periodically using a miniature net radiometer (Type ME-1, Swissteco Pty. Ltd., Melbourne).

Sample plants were sealed in their pots with

plastic bags and weighed at two-hourly intervals during the photoperiod starting before the lights came on and ending after they went off. At the end of each day a volume of water roughly equal to the transpirational loss of each plant was replaced in the pots using a syringe. The sealed pots were also aerated for 30-45 minutes each day, using an air pump, to minimise anaerobiosis. Gains in weight due to  $\text{CO}_2$  assimilation and increases in leaf area over the course of the six day experiments were assumed to be negligible. Transpiration rate was expressed on plan area basis since all sample species were hypostomatous except P. sylvestris. Leaf surface area was measured destructively at the end of each experiment using a Li-Cor area meter (Model 3100).

In the case of P. sylvestris the individual needles were very roughly cylindrical (surface area =  $2\pi rh$ ) and since projected area ( $A_p = 2rh$ ) was measured on the area meter, total surface area should be estimated by  $\pi A_p$ . However, comparison with careful hand measurements of the surface areas of fifty P. sylvestris needles showed the factor to be slightly less than  $\pi$ , probably due to needle taper, and this measured factor of 3.04 was used.

Plants were subjected to daily increases in wind speed from  $0.25 \text{ m s}^{-1}$  to  $5 \text{ m s}^{-1}$ . On the sixth day the wind speed was returned to the lowest value to assess

reversibility of effects.

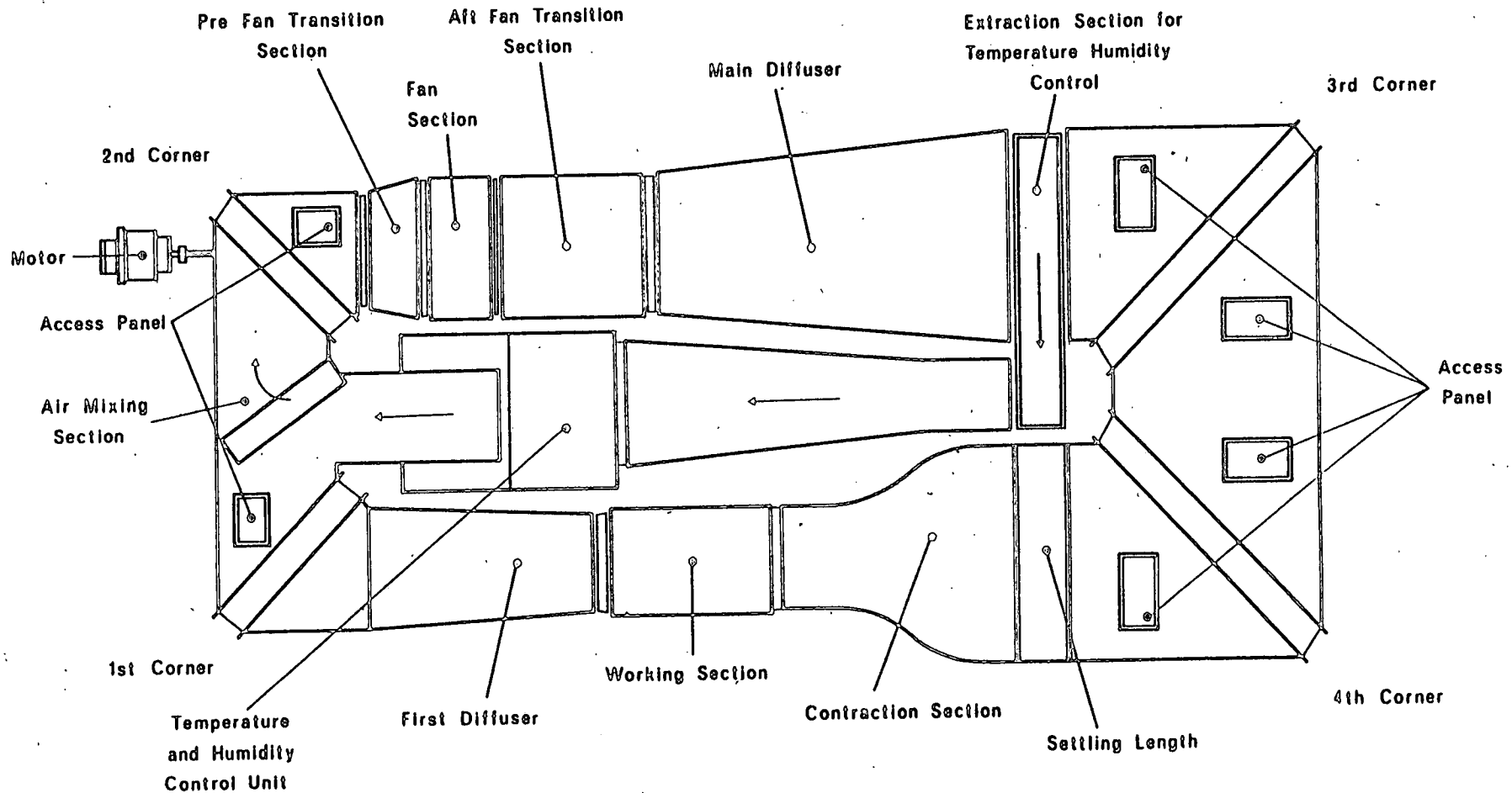
### 2.1.1 The Wind Tunnel

The controlled environment wind tunnel depicted in Fig. 2.1 was used in this study and the following description is based on that of Thompson (1975).

The wind tunnel is a closed-circuit or Prandtl type. Air flow is driven by the main fan situated at the second corner and calibration is achieved using a pitot static tube and a micromanometer (Combustion Instruments, Middlesex). Turning vanes at the corners and the smooth, finished surface of the wind tunnel restrict the development of turbulence. The walls of the rectangular cross-section tunnel are constructed of two layers of marine plywood sandwiching expanded polystyrene, mounted on a steel framework.

Part of the air is extracted at the third corner for temperature and humidity control. Heating and refrigeration units mounted outside the wind tunnel provide a wide, stable range of air temperature. Humidity is regulated by the injection of steam into the air.

Two cylinders, 125 mm in diameter, mounted cross-wise in the throat of the wind tunnel generate artificial turbulence within the working section. This arrangement is known to produce a turbulence intensity of 0.5



( All Access Panels in Underside )

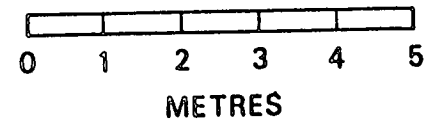


Fig.2.1 The controlled environment wind tunnel in the Department of Forestry & Natural Resources.

(Grace and Wilson, 1976) and was used in all experiments on live plant material. Different crosspieces were assembled for use in experiments on single brass leaf replicas or plant replicas and will be discussed later. u

The 1.8 m x 0.9 m working section can be raised and lowered by electromechanical means for access. It is also accessible through three re-sealable ports in the front, triple-glazed, perspex wall. Li The internal glass walls are lined with silver-coated polyester to increase irradiance. Nine 400 W metal halide lamps and six 60 W tungsten lamps mounted above the glass ceiling provide a quantum flux of about  $250 \mu\text{E m}^{-2}\text{s}^{-1}$  in the 400-700 nm range at a height of 30 cm above the plants.



## 2.2 Temperature Sensing on Leaves

The vapour pressure difference between the sub-stomatal cavity of a transpiring leaf and the ambient air is the driving force for water vapour exchange between leaf and air. It is generally accepted that the air in the sub-stomatal cavity is saturated with water vapour (Monteith, 1965; Linacre, 1967). Therefore an accurate measurement of leaf temperature is required, along with some measure of the absolute humidity of the atmosphere, in order to assess the vapour pressure difference between the leaf and the air.

As simple as this sounds there are considerable difficulties in making a good measurement of leaf temperature. Technically, the problems are at least twofold: (1) sufficient sensitivity of differential temperature measurements to resolve small vapour pressure differences ( $<0.1$  mb) precisely is desirable and (2) the physical properties of the measuring instrument must have a minimal effect on the energy regime of the leaf being measured.

Remote sensing of leaf temperature has been put forward by some authors as a possible solution to the latter problem. Idle (1968) described a simple and economic thermopile radiometer as a remote temperature sensor, and several such instruments are commercially available. Thermography, or thermal image photography,

was used by Thofelt (1975) to investigate leaf temperature. Clark (1975) also presented thermograms of leaf surfaces, both model and real. Studies of this type point out the extent of thermal gradients and the complexity of the energy regime on leaf surfaces.

Among the drawbacks to the use of remote sensing techniques in the present research are the lack of precision compared with thermoelectric methods such as thermocouples or thermistors and the physical bulk of the instrumentation which tends to shade the leaf being measured, thus altering the local energy regime. Finally the prohibitive expense and lack of availability of remote sensing instruments made them an unattractive choice.

The alternative approach is to attach sensors to the leaf. Idle (1968) suggested that thermocouples or thermistors of the smallest practicable size may give good results

"on the grounds of interfering least with the energy and material fluxes, of not plugging up the stomata, and of avoiding the conduction of heat to or from the selected spot."

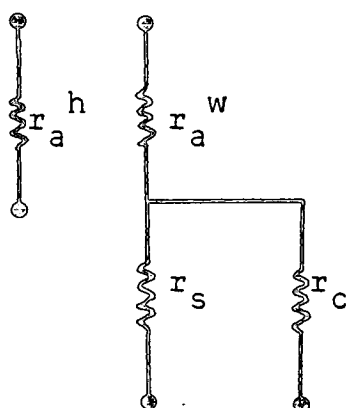
Perrier (1971) discussed the advantages and disadvantages of a number of techniques for measuring leaf temperature. He concluded that with adequate precautions as to sensor size and placement, thermoelectric methods allowed easy, reliable and precise

measurements in most cases. Radiative methods employing remote sensors have particular application in the field (e.g. canopy surface temperature) or in the laboratory (e.g. investigation of thermal field).

Extremely fine soldered thermocouples constructed of copper and constantan wires, 0.05 mm in diameter, were used to measure the surface temperatures of leaves. An average leaf temperature was determined using sixteen such thermocouples randomly situated throughout the canopy bearing in mind temperature gradients within the canopy as well as over individual leaf surfaces (Wigley and Clark, 1974). The sensors, and up to three centimeters of the wire leads, were coated with a thin film of cello tape glue, extracted in chloroform, to act as an adhesive (Idle, personal communication). Wire leads were run along the abaxial surface of the leaf to avoid conduction of heat across the boundary layer, in the wires. It was considered that the coating of glue would increase the emissivity of the sensor to nearly unity, so that the thermojunction would be coupled to the leaf by both conductive and radiative heat exchange. The thermocouples were connected to a recording device with an electronic reference (Kent, Mark 3 Electronic). Calibration was checked from time to time with a Gold Line thermometer graduated in tenths of a degree. No substantial errors, such as those arising from slightly dissimilar batches of wire or induced e.m.f.'s, were encountered.

### CHAPTER 3. Measurement of Aerodynamic Resistance/ Conductance

Transfer of sensible heat occurs across the boundary layer at the leaf surface and is driven by the gradient of temperature. Mass transfer, driven by a concentration gradient, also occurs across the boundary layer, though in most cases (as in water vapour) there is an additional length of diffusion path corresponding to the stomatal pores and their associated substomatal cavities. Conventionally, this situation is represented by an electrical analogue:



where  $r_a^h$  = the aerodynamic resistance to heat transfer

$r_a^w$  = the aerodynamic resistance to mass (i.e. water vapour) transfer

$r_s$  = the stomatal resistance

$r_c$  = the cuticular resistance

The latter is often neglected since it is so large in most cases that insignificant fluxes occur through the cuticle. An exception to this occurs when wind and abrasion cause cuticular damage and appreciable quantities of water vapour are lost by evaporation through the cuticle (Grace, 1974; MacKerron, 1976).

The effect of wind on transfer processes depends on the quantitative relationship between aerodynamic resistance and windspeed, and also on the relative magnitudes of aerodynamic and stomatal resistances. One of the purposes of this investigation was to estimate the quantitative relationships between these variables under varying environmental conditions.

Recently, it has become more usual to speak of conductance,  $g$ , rather than resistance; where  $g = \frac{1}{r}$ . Conductance and transfer rates are directly proportional. On the other hand, resistances are additive when they are in series so that the total diffusion resistance of a linear diffusion path can easily be evaluated as the sum of its separate components. Hence, there is no strong reason for choosing either resistance or conductance at the exclusion of the other and both terms are used here.

The aerodynamic and stomatal resistances may be estimated by using the approach first introduced by Gaastra (1959). Namely, determine the transpiration flux so that total resistance ( $r_a + r_s$ ) can be found:

$$r_a + r_s = \frac{\chi_L - \chi_a}{E} \quad (3.1)$$

where  $E$  = water vapour flux ( $\text{kg m}^{-2}\text{s}^{-1}$ )  
 $\chi_L$  = concentration of water vapour in the  
 substomatal cavity ( $\text{kg m}^{-3}$ )  
 $\chi_a$  = concentration of water vapour in the  
 air ( $\text{kg m}^{-3}$ )

Then a model of the leaf is prepared so that the aerodynamic component of the resistance pathway can be isolated by estimating the flux of a suitable diffusing species across a boundary layer like that of the leaf. In general:

$$r_a = \frac{\chi_o - \chi_a}{F} \quad (3.2)$$

where  $r_a$  = aerodynamic resistance to transfer of  
 the diffusing species ( $\text{s m}^{-1}$ )  
 $\chi_o$  = concentration of the diffusing species  
 at the model surface ( $\text{kg m}^{-3}$ )  
 $\chi_a$  = concentration of the diffusing species  
 in the ambient air  
 $F$  = flux of the diffusing species ( $\text{kg m}^{-2} \text{s}^{-1}$ )

Gaastra (1959) originally used water vapour as the diffusing species, thus  $r_a = r_a^w$  and this value can be

substituted in equation (3.1) to allow calculation of  $r_s$ .

Since Gaastra's work other methods have been devised to evaluate the resistances or conductances for heat and mass transfer but the basic approach has remained the same.

### 3.1 Technical Evaluation

#### 3.1.1 Stomatal Component of Mass Transfer ( $r_s$ or $g_s$ )

The most widely used technique for the estimation of stomatal resistance is diffusion porometry (Kanemasu, et al. 1969; Turner and Parlange, 1970; Beardsell, et al. 1972). Jarvis (1981) provides a concise evaluation of the applications and limitations of this technique. For the reasons expressed above (Chapter 2), it was undesirable to use the porometer in this study and  $r_s$  was found from a knowledge of  $r_a$ ,  $E$ ,  $X_L$  and  $X_a$  by applying equation (3.1). An advantage of this method is that the  $r_s$  value obtained is an average for all leaves on the plant, whereas, at best, the porometer can only provide an estimate of the resistance of a small sample of the leaves. In practice, systematic errors arise because of heating of the leaves in the enclosed chamber. These errors are likely to be dependent on the species under test as they will be a function of the energy balance of the leaf when the chamber is closed (Parkinson and Day, 1980).

#### 3.1.2 Aerodynamic Component of Mass Transfer ( $r_a^w$ or $g_a^w$ )

The aerodynamic component of the resistance/conductance pathway is technically a difficult quantity



to measure and has given rise to considerable uncertainty in the literature (e.g. see Monteith, 1981). For measurement purposes, the most common analogous system to be reported is that of a leaf model, made of filter paper and soaked with water (Gaastra, 1959; Jarvis, 1971; Grace and Wilson, 1976; Murphy and Knoerr, 1977). Careful weight, temperature and humidity measurements are required to solve the form of equation (3.2) where  $r_a = r_a^w$ ,  $X_o$  and  $X_a$  are respectively the water vapour concentrations at the model's surface and in the ambient air ( $\text{kg m}^{-3}$ ) and  $F$  is the flux of water vapour ( $\text{kg m}^{-2}\text{s}^{-1}$ ). The value of  $X_s$  can be found in tables assuming that the air immediately above the water film is saturated at that temperature.

The disadvantages of this technique include errors resulting from evaporation during weighing, formation of water droplets, temperature gradients on the model surface, and simply the practical problems of manipulating the system successfully within a controlled environment. Grace and Wilson (1976) pointed out that the main source of error in the evaporation technique was that arising from the difficulties in accurately knowing the vapour pressure at the model leaf surface and in the air. As the difference between these constitutes the driving force for evaporation, errors in both very seriously influence knowledge of this driving force. Overall, the errors in the aerodynamic

conductance in their experiment could have been as high as 45% (Grace and Wilson, 1976).

A mass-transfer analogue technique which uses a thin film of naphthalene is an alternative (Neal, et al., 1970; Lewis, 1971; Neal, 1975). In this case, naphthalene replaces water as the diffusing species. Its rate of sublimation can be measured by careful weighing. The main advantage of this technique is that the heat of sublimation is so small that the system hardly cools at all. Thus temperature measurements are not required. Moreover, the pattern of naphthalene removal provides information on the local variation in  $r_a$  on the leaf surface. When used outdoors there is no need to measure ambient concentrations, as naphthalene is not a normal constituent of the air. However, since the controlled environment wind tunnel in which these experiments were to take place is a closed system, gradual build-up of naphthalene vapour pressure would adversely affect the measurements. This consideration tended to eliminate the use of any other techniques requiring volatile agents even though some of these would have provided certain advantages.

The electrochemical mass-transfer analogue provides flow visualisation and estimates of diffusive resistance/conductance (Hanratty, 1969; Schuepp, 1972, 1973). In this technique, the leaf model is used as the anode or cathode in an electrolysis bath. Hence, the diffusing

substances are ions and the diffusing medium is water. Proponents of this technique point out that this should not matter when data are to be analysed using non-dimensional groups, since such factors as ion diffusivity and the viscosity of the fluid are taken into account. However, Neal (1975) advised considerable caution in interpreting the results as it is his contention that the analogy is tested much more severely when the diffusing medium differs widely from air in physical characteristics. Within the context of these wind tunnel experiments it was felt that an electrochemical system might not provide a very reliable guide to diffusion rates in air, even after correction for the differences in the diffusion coefficients.

In view of the difficulties inherent in making good measurements of  $r_a$  for water vapour ( $r_a^w$ ), it was decided instead to concentrate attention on  $r_a$  for heat ( $r_a^h$ ) and then convert to  $r_a^w$  using a well-known relationship (Equation (1.8)).

### 3.1.3 Aerodynamic Component of Heat Transfer ( $r_a^h$ or $g_a^h$ )

Many authors have chosen to express the aerodynamic component of the resistance/conductance pathway for heat in terms of a heat transfer coefficient.

In general:

$$h_c = \frac{F}{T_L - T_a} \quad (3.3)$$

where  $h_c$  = the heat transfer coefficient  
( $J\ m^{-2}s^{-1}^{\circ}C^{-1}$ )

$T_L$  = the temperature of the leaf surface ( $^{\circ}C$ )

$T_a$  = the temperature of the ambient air ( $^{\circ}C$ )

A review of heat transfer from leaves is provided by Raschke (1960). Linacre (1964) derived a simple formula for the heat transfer coefficient of a leaf as it cools from an initial temperature  $T_o$  to a temperature  $T_1$  in time  $t$ , and this is given by:

$$h_c = \frac{m C_L}{L t} \ln \frac{T_o - T_a}{T_1 - T_a} \quad (3.4)$$

where  $m$  = the mass of the leaf

$C_L$  = the specific heat of the leaf material

$L$  = the total surface area of the leaf

$T_a$  = the ambient air temperature

Tibballs, et al. (1964) overcame the problem of the complex geometry of a conifer shoot by using silver castings and determining heat transfer coefficients by allowing the models to cool through large temperature excesses ( $>30^{\circ}C$ ). The low emissivity of silver reduced the importance of the radiation component of heat transfer. Surface areas were determined by electrolytic techniques.

Kumar and Barthakur (1971) measured convective heat transfer from real leaves in a wind tunnel and found heat transfer coefficients higher than those calculated from laminar boundary layer theory. Leaves with rough surface elements were found to further increase the discrepancy between observed and predicted transfer coefficients. Also, when plotting the logarithm of temperature excess against elapsed time they observed a consistently non-linear portion at high temperature differences ( $>4^{\circ}\text{C}$ ). This did not altogether disappear even in wind velocities up to  $5\text{ m s}^{-1}$ .

It is no longer usual, except in certain engineering texts, to express heat transfer as  $h_c$ , the heat transfer coefficient. Dimensionally, aerodynamic conductance in  $\text{m s}^{-1}$  or resistance in  $\text{s m}^{-1}$  are more compatible with stomatal conductance or resistance. Since this study was aimed at separating the effects of environmental variables on , in particular, the stomatal and aerodynamic components of the diffusion pathway, it was found more convenient to use conductance ( $g_a$ ) or resistance ( $r_a$ ) than the heat transfer coefficient ( $h_c$ ).

Conductance may be expressed as:

$$g_a = \frac{F}{\rho C_p (T_L - T_a)} \quad (3.5)$$

where  $\rho$  = the density of air ( $\text{kg m}^{-3}$ )  
 $C_p$  = the specific heat of air at constant  
pressure ( $\text{J kg}^{-1} \text{ } ^\circ\text{C}^{-1}$ )

Hence, by comparing equations (3.3) and (3.5) the relationship between conductance ( $g_a$ ) and heat transfer coefficient ( $h_c$ ) is:

$$h_c = \rho C_p g_a \quad (3.6)$$

Grace, et al. (1980) measured cooling rates of brass leaf replicas to estimate aerodynamic conductance using the formula:

$$g_a = \frac{b w m}{\rho C_p L} \quad (3.7)$$

where  $b$  = the specific heat of brass ( $\text{J kg}^{-1} \text{ } ^\circ\text{C}^{-1}$ )  
 $w$  = the mass of the brass model (kg)  
 $m$  = the slope of the regression of the  
logarithm of the leaf-air temperature  
difference against time ( $^\circ\text{C } ^\circ\text{C}^{-1} \text{ s}^{-1}$ )  
 $L$  = the total surface area of the model ( $\text{m}^2$ )

The technique was found to yield highly reproducible values of  $g_a$  and the main source of error - that of radiative dissipation of heat - was acceptably low when the metal was polished to reduce its emissivity, and the temperature excess kept small ( $<3^\circ\text{C}$ ).

### 3.2 The Cooling Curve Technique

Estimates of aerodynamic conductance/resistance were obtained using, with only minor alterations, the cooling curve technique of Grace, et al. (1980). A correction factor of 0.924 was used to convert  $g_a^h$  to  $g_a^w$  (Jarvis, 1981).

Leaf replicas were cut from brass sheet ranging in thickness from 0.10mm to 0.25 mm and polished to a measured emissivity of 0.10. Soldered copper-constantan thermocouples constructed of 48 S.W.G. wire (0.05 mm diameter) were attached to the underside of the leaf replicas by coating the wires with cellotape glue extracted in chloroform (Idle, personal communication). To reduce conduction to or from the junction, 2-3 cm of the wires were stuck to the replica. The reference junctions were encased in a small amount of putty (Blue Tac) to reduce their response time, and placed in the air impinging on the leaf model. A radiant heater constructed of resistance coils was used to heat the model leaves 2.5 to 3.0 °C above ambient temperature. These experiments were carried out in the dark to limit radiation coupling. Amplified thermocouple output was recorded on a potentiometric chart recorder (Model 28000, Bryans-Southern, Mitcham, Surrey) which was calibrated using a constant voltage source (Model 404, Time Electronics, Tonbridge, Kent). The resulting

exponential relationship between temperature difference ( $\Delta T$ ) and time, as the brass leaf cooled to ambient, was used to calculate aerodynamic conductance, as above. The relationship between  $\ln \Delta T$  and time was always linear as long as  $\Delta T$  did not exceed  $3^{\circ}\text{C}$ . The correlation coefficient was typically -0.9998 whilst the slope was reproducible to within 0.1%. Typical examples of the plot of  $\ln \Delta T$  versus time are given in Grace, et al. (1980).

The success of the technique depended greatly on the reliable and sensitive amplification of the thermocouple outputs. To achieve this an electronic circuit was designed and constructed (circuit diagram and components list in Appendix A). The resulting instrument was capable of resolving small temperature differences with a typical accuracy of  $\pm 0.01^{\circ}\text{C}$ . In the short term, no appreciable thermal instability or zero drift occurred. Such a high degree of resolution allowed for minimal perturbation of local energy regimes when obtaining cooling curves since only small temperature excesses were required in the leaf models.

To provide as realistic a physical environment as possible, brass leaf replicas replaced real leaves of similar shape and size in the canopies of the sample species (e.g. Plate 3.1). Brass leaves were also used to investigate the influence of leaf minutiae (Plate 3.2) and leaf juxtaposition (Plate 3.3) on aerodynamic conductance.





Plate 3.1 A brass leaf replica replacing a real leaf of Faqus sylvatica in the canopy.

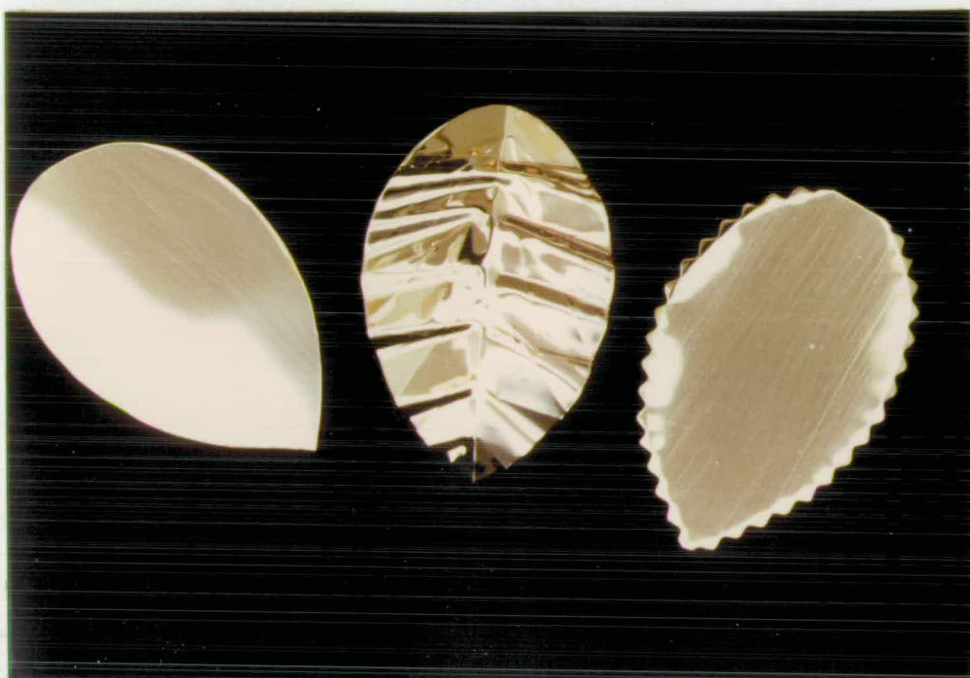


Plate 3.2 Three brass leaf forms, from left to right:  
smooth, rippled and serrated.

(a)



(c)



(b)



Plate 3.3 Configurations of brass leaves: (a) lax, (b) bunched, (c) swept.

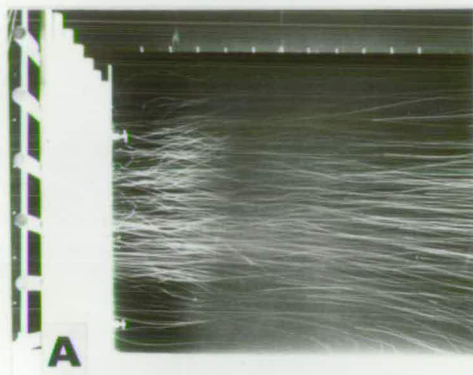


The desire to simulate realistic exchange conditions still further, called for a turbulent wind regime. The characteristics and effects of various turbulent wind regimes on brass leaf models were evaluated. Three sizes of turbulence generating crosspieces were constructed (23 mm, 60 mm and 110 mm diameter). Flow visualisation, using a helium bubble generator (Armfield Engineering Ltd., Hampshire, England) was employed to aid qualitative distinction between the types of turbulence produced by each set of crosspieces (Plate 3.4). This was coupled with an energy spectrum analysis of the turbulence frequencies produced using a spectrum analyser (Hewlett-Packard, Model 3582A). The sensing instrument for spectrum analysis was a constant temperature hot wire anemometer with linearizer (Disa, Model 55K). It was used to evaluate the turbulence spectrum of each set of crosspieces as well as that produced near the surface of each of the leaf forms under various turbulence regimes discussed later (Chapter 5). Energy spectra of the turbulent boundary layer over each leaf form was measured at a height of 1 mm over the upper surface of the replica, near its centre.

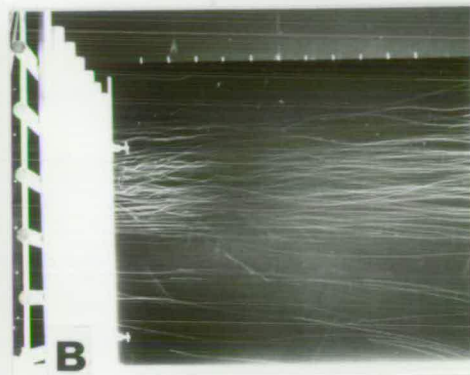
Plate 3.4 Flow visualisation through three sizes of crosspieces using helium filled soap bubbles in a wind tunnel. A and B show small crosspieces; C and D, medium crosspieces; E and F, large crosspieces. The scale units at the top of each photograph are decimeters.



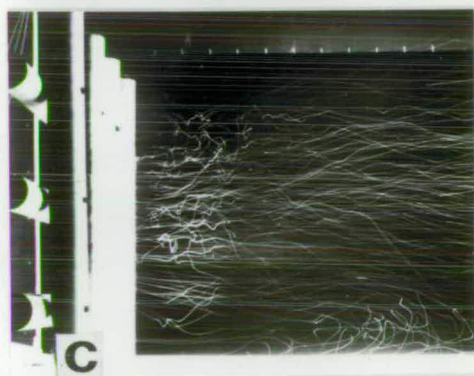
$u = 1 \text{ m s}^{-1}$



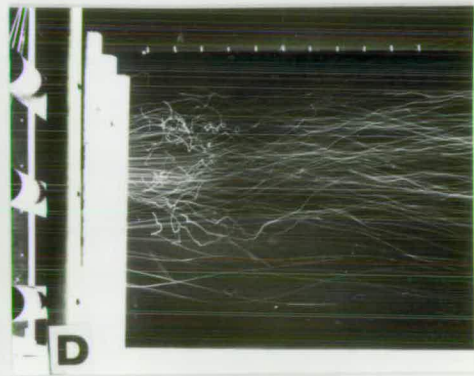
$u = 2 \text{ m s}^{-1}$



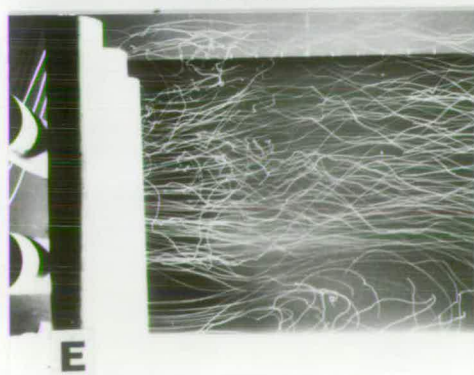
$u = 1 \text{ m s}^{-1}$



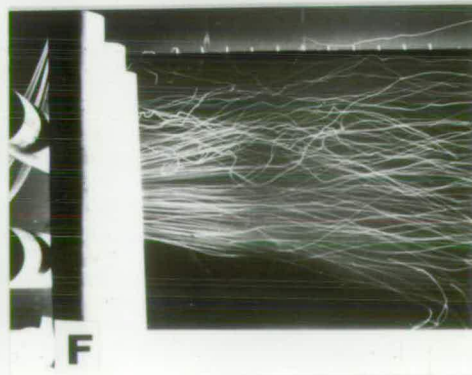
$u = 2 \text{ m s}^{-1}$



$u = 1 \text{ m s}^{-1}$



$u = 2 \text{ m s}^{-1}$



## CHAPTER 4. Measurement of Components of Water Potential.

### 4.1 Technical Objective

The design of the experiments for investigating the effects of wind on the water status of small trees required a technique to measure water potential (and preferably its components). This technique must use only small amounts of leaf tissue so that sampling does not substantially reduce leaf area, and it should enable replicate determinations at any one time. Three separate methods of obtaining these objectives were assessed. In two cases the techniques were taken from the stage of instrument development, to calibration and trials under experimental conditions.

#### 4.1.1 Pressure Bomb Technique

The pressure bomb (or chamber) provides, by far, the simplest and most direct method of measuring the total water potential of plant tissue. Results using this technique are extensively reported in the literature (Scholander and Hammel, 1965; Tyree and Hammel 1972) and it is generally accepted as the basis of comparison for all other techniques.

The major disadvantage of the pressure bomb as a tool in the experiments reported here is that it requires

too much plant tissue. Only when specimens of P. sylvestris, with their relatively large number of leaves for samples, were used as experimental subjects was this technique useful for the fast determination of total water potential. In broad-leaved species the removal of individual leaves, or leaflets, over the course of a week would have consumed a substantial part of the total leaf area.

The components of water potential may also be measured with a pressure bomb by generating a pressure-volume curve (Tyree, et al. 1972; Hellkvist, et al. 1974) and by extrapolation, determining the values of the turgor and osmotic potentials. This, however, is a time-consuming and arduous task, which in any case has been criticised on both experimental and theoretical grounds (Acock, 1975).

The pressure bomb technique was therefore not extensively used as a means of obtaining measurements of water potential, but occasionally used for comparison with other methods.

#### 4.1.2 Impedance Technique

Electrical measurements in plants have advantages over many other techniques in that they can be carried out in the living organism, in situ, and without destroying tissue. In dealing with living tissue,



interpretation of results is difficult unless the pathway followed by the measuring current is predominantly apoplastic, as in xylem and multicellular isodiametric tissue (e.g. certain giant algae) (Fensom, 1966; Hayden, et al. 1969; Hayden, et al. 1972). Also, it has been shown that pulsed DC or low frequency AC will mostly flow in an apoplastic pathway (Hayden, et al. 1969; Scutt, et al. 1972) without producing appreciable polarising effects at the electrodes. The question remains as to what fundamental properties of the apoplast control the value of electrical impedance. Nevertheless, Dixon, et al. (1978) reported a linear relationship between impedance and total water potential, measured with a pressure bomb and a thermocouple psychrometer, in Persea americana Mill. and Picea glauca (Moench.) Voss.

It was decided to investigate the usefulness of the impedance technique further as a means of continuously monitoring total water potential in experimental plants. An instrument was designed and constructed capable of measuring tissue temperature, as impedance is temperature dependent, and impedance at a constant two microamps AC. (Fig. 4.1).

Attempts to calibrate the instrument against the pressure bomb using P. sylvestris were promising (Fig. 4.2). However, inherent problems with the technique made its routine application more difficult than anticipated. Distance between electrodes and diameter

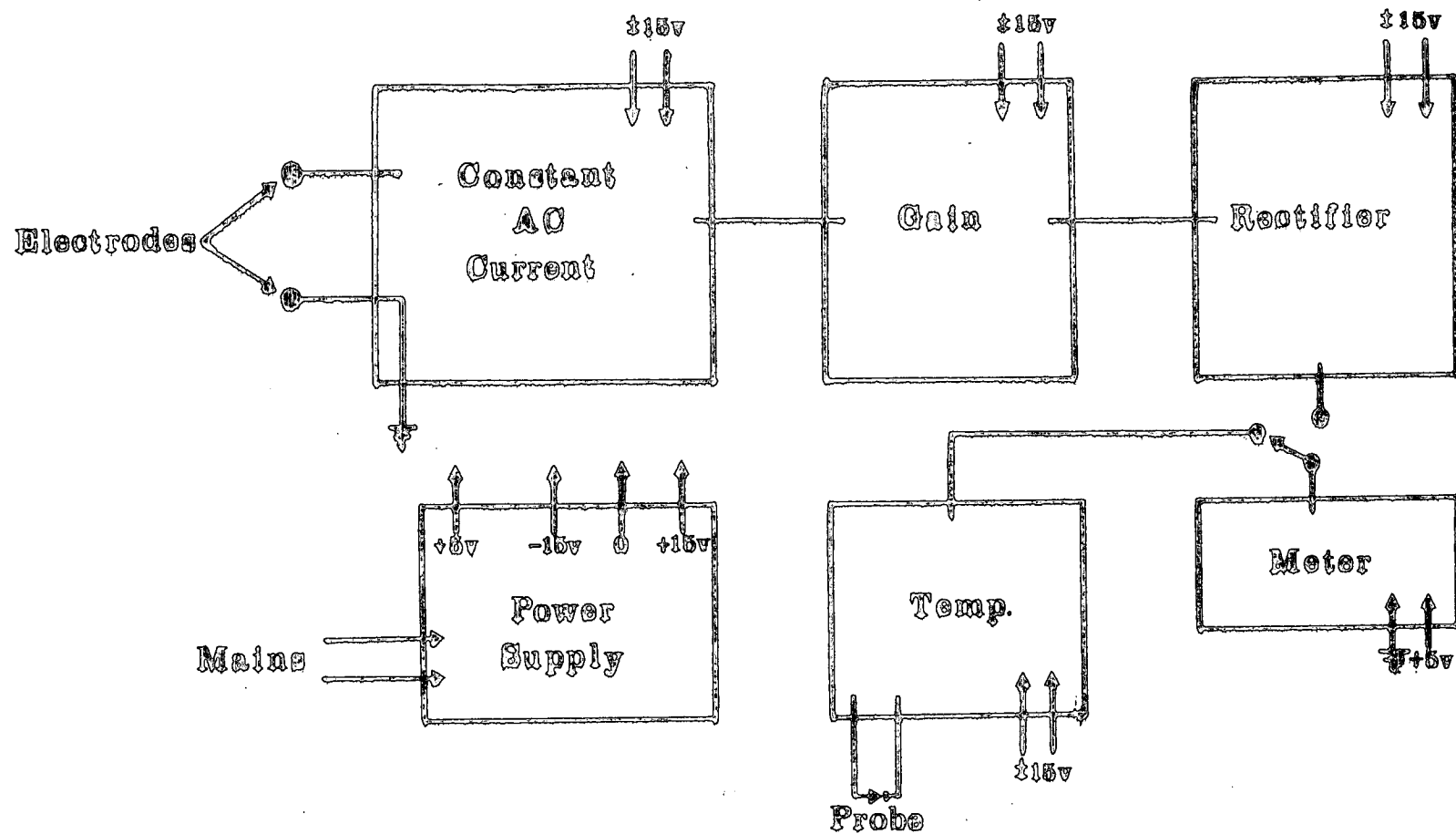


Fig.4.1 Block diagram of impedance and temperature measuring instrument.

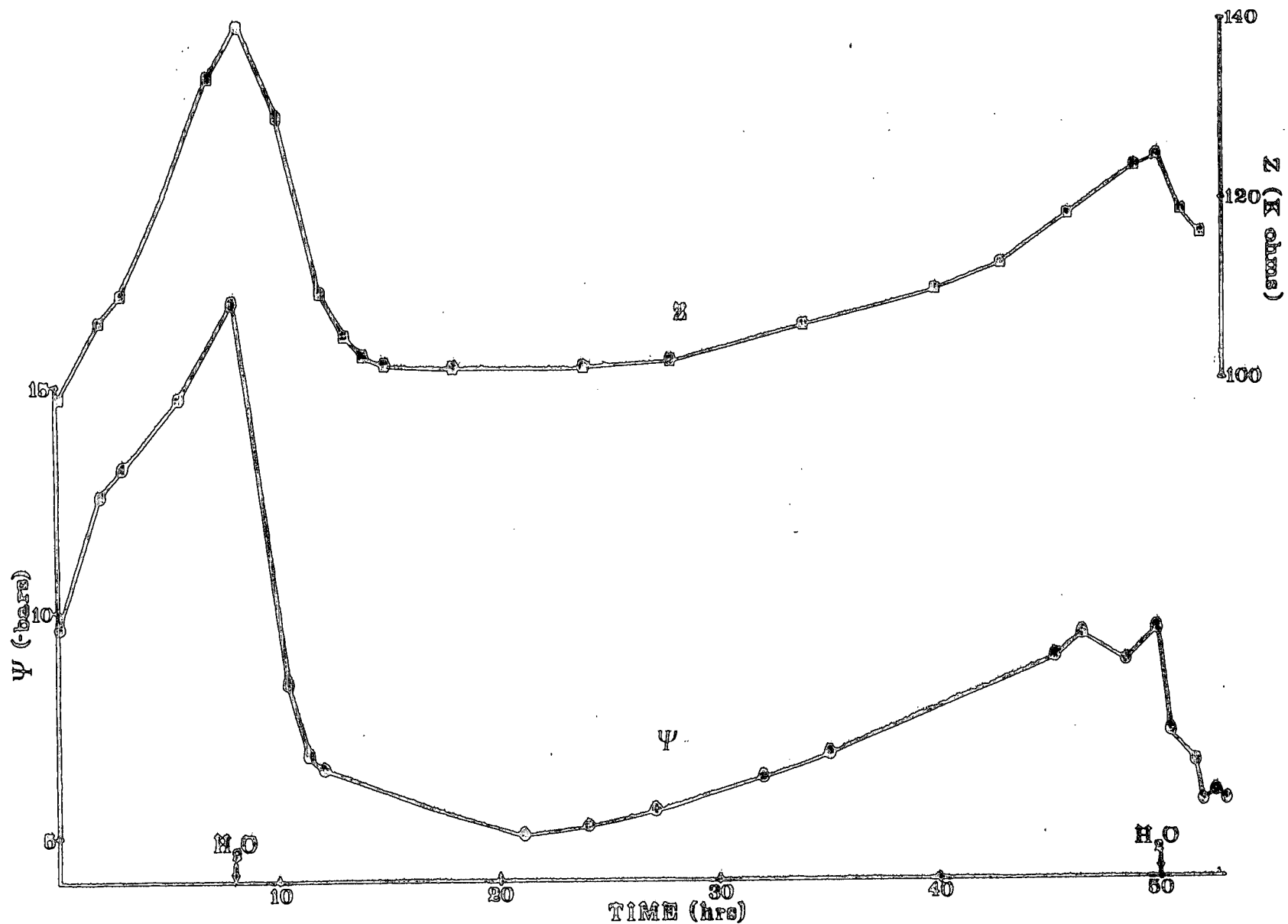


Fig.4.2 Concurrent measurements of impedance (Z) and total water potential ( $\Psi$ ) in Pinus sylvestris.

of the branch, and thus the current pathway, may vary from trial to trial so that separate calibration is required each time. Anatomical differences in the tissue between the electrodes, metabolic reaction to injury, as well as varying degrees of embolism around the sites of implantation pose further problems of drift in the calibration. These factors make the interpretation of the absolute impedance readings in a given trial impossible to relate to those in another trial under similar conditions of water potential and temperature. Finally, this technique is limited in that even though it may be calibrated against the pressure bomb, it does not allow measurement of the components of water potential.

#### 4.1.3 Thermocouple Psychrometry

Recently the thermocouple psychrometer (Spanner, 1951) has become a common research tool among plant physiologists. The technique involves enclosing a section (excised or entire) of plant tissue, usually leaf, within a sealed chamber and allowing it to achieve vapour pressure equilibrium with the chamber air. Then a tiny thermocouple junction in the chamber is cooled by a Peltier cooling current condensing a droplet of water onto the junction. Once the cooling current is turned off the temperature difference between the

thermocouple junction and the chamber caused by the evaporating water is measured by a sensitive micro-voltmeter. The evaporation of the water droplet is dependent on the relative humidity within the chamber which, in turn, is determined by the water potential of the sample. Furthermore, if the sample is then removed and its cells disrupted by freezing, boiling or mashing before returning it to the chamber for further equilibration, one may then measure the osmotic potential. The other important component of water potential, turgor, can be obtained by difference, since:

$$\Psi = P - \Pi - T$$

where  $\Psi$  = total water potential

$P$  = turgor potential

$\Pi$  = osmotic potential

$T$  = matric potential

( $T$  is usually considered together with  $\Pi$  in leaf tissue.)

Hence, we have a seemingly comprehensive technique for measuring water potential and its major components.

There are several reviews on the application of the Spanner psychrometer for evaluating plant water status (Rawlins, 1966; Barrs, 1968; Peck, 1968, 1969; Boyer, 1969; Brown, 1970). Also, there are practical

guides on the use and modification of the thermocouple psychrometer (Wiebe, et al. 1971; Millar, 1970(a), 1970 (b), 1973).

The obvious versatility of the thermocouple psychrometer with reference to this research made it an attractive choice. Its requirement for plant tissue was slight compared with the pressure bomb and it provided a relatively easy method of measuring the components of water potential. However, in order to avoid the expense of commercially available chambers, especially as large numbers were required for replication of measurements, it was necessary to embark on an extensive construction and testing program.

Within the framework of developing a satisfactory thermocouple psychrometer a number of subsidiary investigations, which are of general interest to researchers in this field, have resulted. These will be reported in later sections (4.2 and 4.3).

#### 4.1.4 Other Techniques

Measurement of the relative attenuation of gamma or beta radiation as it passes through plant tissue is another possible method of assessing water content (Woods, et al. 1965; Edwards, 1981). Another method is the gravimetric technique described by Barrs (1968), wherein leaf discs are weighed, floated on distilled

water until saturated, reweighed, oven-dried and weighed a final time to give a measure of the relative water content. However, neither of these techniques gives a direct measure of the thermodynamic quantity of water potential; neither do they allow one to separate the components of water potential.

## 4.2 Design and Construction of Thermocouple Psychrometer

### 4.2.1 Design

Commercially available chambers comprise a single sealed chamber and measuring junction. Since equilibration times of plant tissue have been found to be about 3-7 hours (Millar, 1973) and even 12-24 hours for certain tissues (Millar, 1973; Talbot, et al. 1975) then it is easy to see that at least four or five chambers are required to measure a simple diurnal cycle of total water potential changes. Even that number would not satisfy a minimal replication requirement in which proper statistical treatment of the data was planned. Therefore a multiple chamber unit was designed (Fig. 4.3) comprising three separate sealed chambers, hence the name 'Triple' (Plate 4.1). The sample holder and thermocouple mount were constructed of chromium plated brass and threaded for ease of adjustment or removal. All three chambers were housed in two halves of an aluminium block which acted as a stable thermal mass for the reference temperature. The wire leads for each measuring junction were channelled through the aluminium to reduce heat conduction to or from the junction. A large thumb screw provided the sealing force for the three chambers.



Fig.4.3 TRIPLE PSYCHROMETER CHAMBER

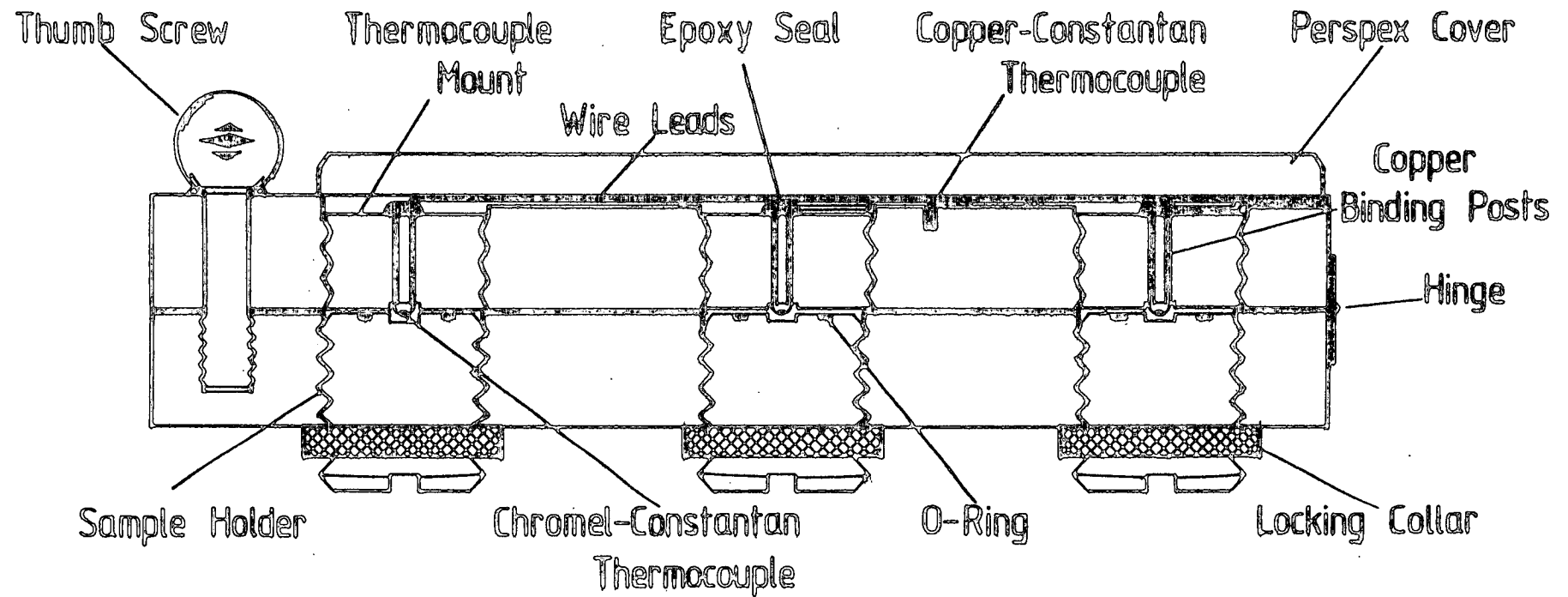




Plate 4.1 'Triple' psychrometer chamber.



#### 4.2.2 Thermocouples for Psychrometer Chambers

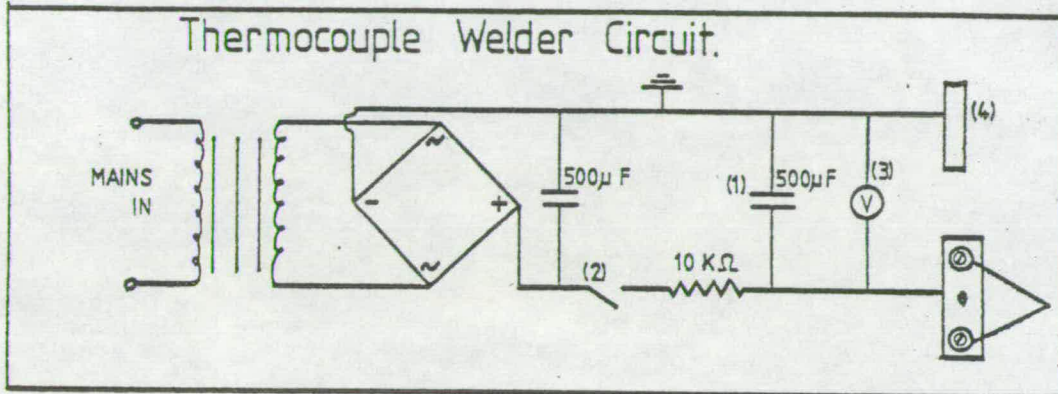
The delicate chromel/constantan thermocouple junction in a psychrometer chamber is the most important part of the instrument and also poses the most difficult construction problems. The necessarily small size of the wires (0.025 mm diameter) prohibits rough handling. The number of chambers required would inevitably result in thermocouple wastage in construction, therefore, it was desirable to be able routinely to produce large numbers of high quality thermocouples.

Construction of the measuring junction has been outlined by Merrill, et al. (1968), Campbell, et al. (1968), Brown, (1970), Lopushinsky and Klock, (1970), Wiebe, et al. (1971). Various techniques have been employed to obtain the initial twisted junction but a simple and successful one, using a special tying rig, is shown in Fig. 4.4. A beaded junction is the desired result and a number of welders and welding techniques, as described in the above literature, have been used to obtain this. Common to many of these techniques is the high failure rate in producing acceptable thermocouples.

Minor alteration to a common welder circuit provides a system which can greatly enhance the success rate of thermocouple production (Fig. 4.5). It was realised that there exists an optimum voltage drop across the welder output terminals which will result in



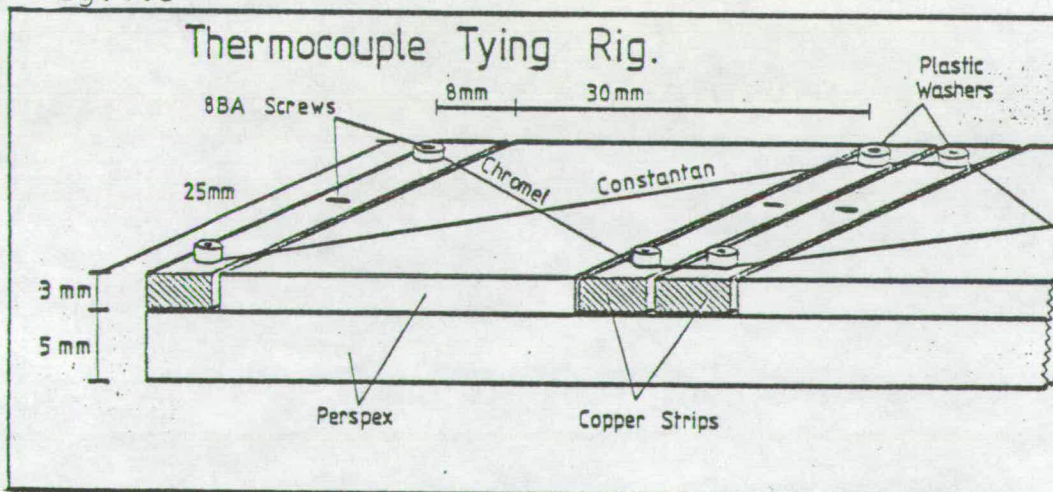
Fig.4.4



**Parts List:**

- 1 x 12V Transformer (6VA)
- 1 x Rectifier
- 2 x 500 uF (50V) Capacitors
- 1 x 10K Resistor
- 1 x Single Pole Switch
- 1 x Carbon Rod (dry cell core)
- 1 x Voltmeter

Fig.4.5



a successful weld. For chromel and constantan wires (0.025 mm diameter) joined with 2.5 twists, this optimum voltage is 28-32 v DC. By monitoring the charged state of the capacitor (Fig. 4.5, (3)) on a voltmeter, one can reproduce ideal welding conditions indefinitely.

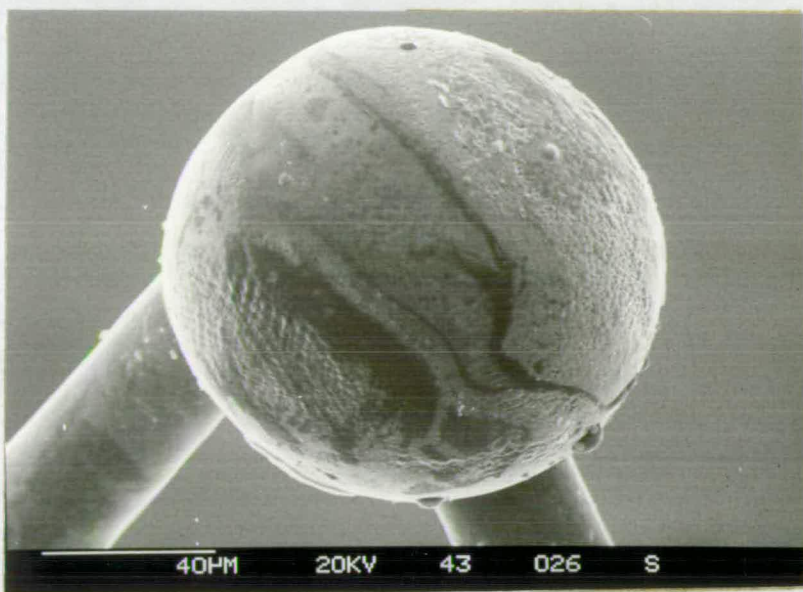
A major source of difficulty in psychrometry is measuring junction failure. This may occur for a variety of reasons including broken junctions and contaminated thermocouples due to deposits of salts, oxides or greasy substances. Detection of a broken thermocouple junction is as obvious as the solution but contamination may prove to be a more subtle and elusive fault.

When welding, critical inspection under a microscope and selection of acceptable junctions can avoid misshapen or oxide-encrusted thermocouples. Plate 4.2 shows typical 'good' and 'bad' thermocouples. Note the clean spherical geometry of the acceptable junction. This enhances the even deposition of a condensed film of water during Peltier cooling as well as even evaporation. Non-spherical, oxide-encrusted thermocouples often produce erratic output and inconsistent results. This may be due to an uneven deposition of condensate resulting in 'patchy' thermal effects on the surface of the thermocouple.

Contamination is probably the most serious fault as it is often difficult to spot and generally becomes progressively worse. A regular cleaning routine of



(a)



(b)

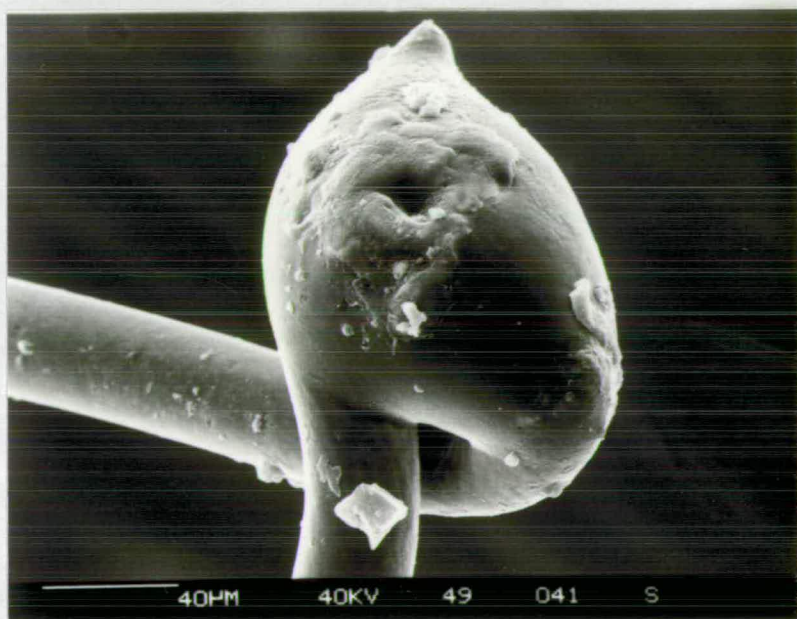


Plate 4.2 Welded chromel-constantan thermocouples:  
(a) an acceptable junction for use in a  
psychrometer chamber (b) an unacceptable  
junction.

psychrometer chambers and junctions should be adopted to minimise this hazard and incorporation of trouble-shooting techniques into normal instrument use is preferred. Using a potentiometric recorder to monitor the output of the measuring junction affords one a continuous check on the state of the thermocouple. Periodic insertion of a reasonably dry calibration sample (0.5 Molal) allows even closer scrutiny of changes in thermocouple output due to contamination (Fig. 4.6).

All these precautions were routinely adhered to when using the psychrometer in the present study.

#### 4.2.3 Calibration

Calibration of the 'Triple' psychrometer chambers was achieved using standard NaCl solutions ranging in concentration from 0.1 Molal to 0.5 Molal. Filter paper discs (Watmans No. 1) soaked in the calibrating solution were equilibrated in each chamber for at least thirty minutes. Figure 4.7 shows the results of a typical calibration.

The chambers were connected to a Wescor HR-33T Microvoltmeter which was operated in both psychrometric and dew point modes (Wescor, Incorporated, 1974). Calibration data and measurements of unknown samples were obtained in this way as a means of cross-checking each reading. This was also useful as a trouble-shooting exercise (Section 4.2.2).



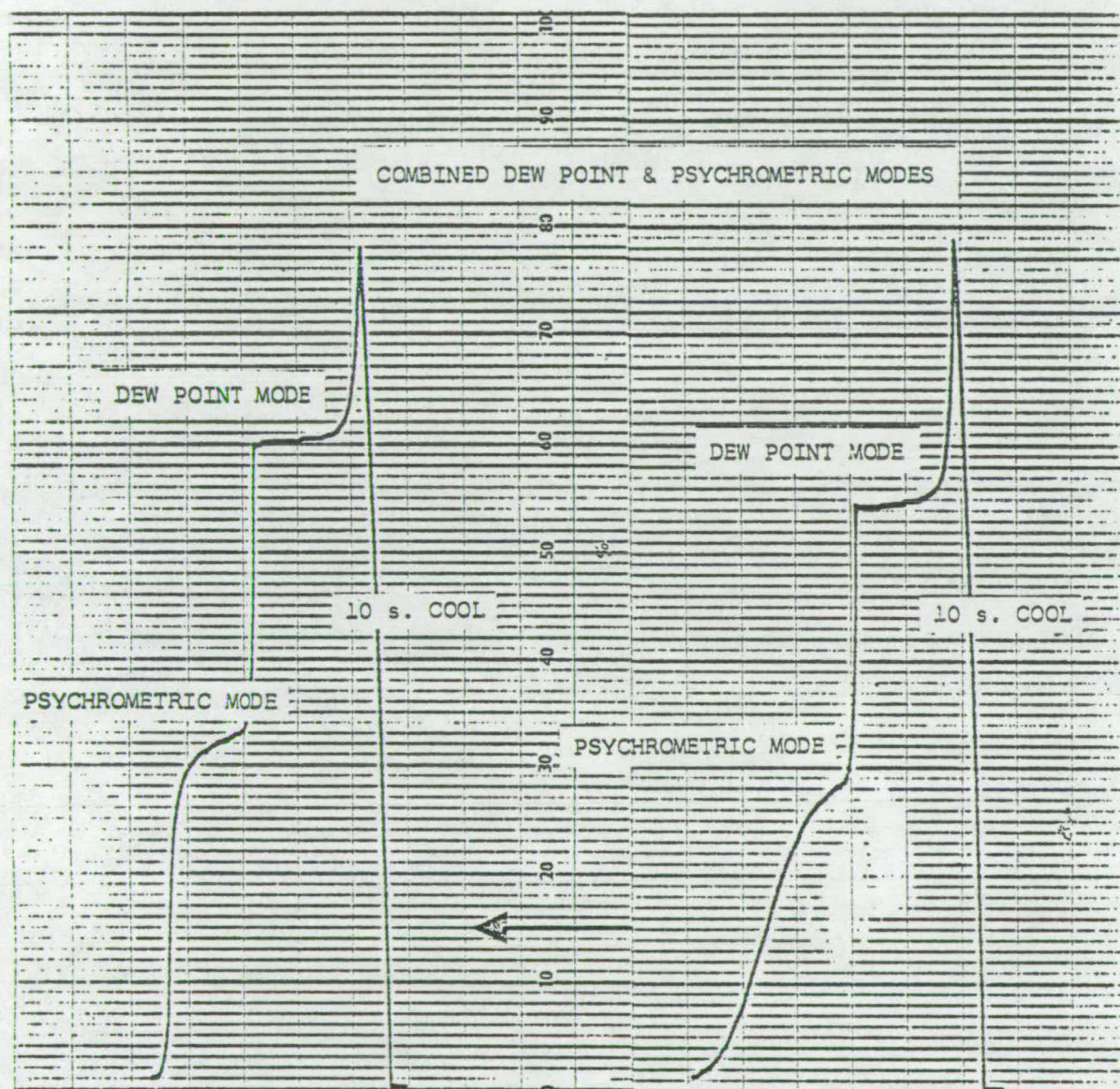


Fig. 4.6 Chart recording of thermocouple output (F.S.D.=30uV Chart Speed =3cm/min.). In both cases, .5 Molal NaCl was the calibration solution and a 10s. cooling time was used. The trace on the right depicts a "dirty thermocouple" while that on the left is the output from the same thermocouple following cleaning. Note the increased sensitivity and distinct psychrometric plateau of the cleaned thermocouple.



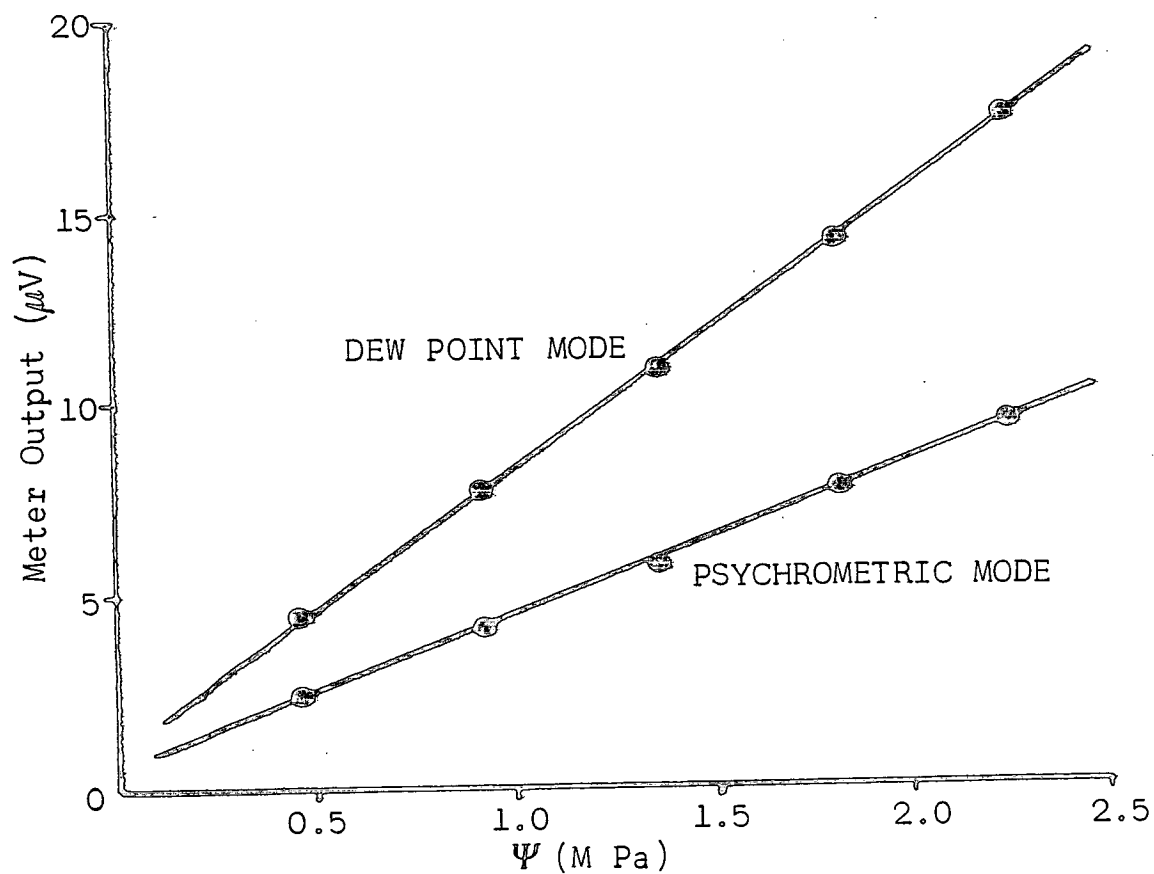


Fig.4.7 Typical calibration for the 'Triple' psychrometer chamber using 0.1, 0.2, 0.3, 0.4 and 0.5 molal NaCl solutions at 25 °C.

#### 4.3 Water Uptake by Some Chamber Materials

A potential source of error in measurements made with a thermocouple psychrometer chamber is the ad/absorption properties of the chamber material. In particular, the equilibrating chamber air is in contact with the inner chamber walls and a portion of the sealing gasket or O-ring. Should these surfaces take up a significant proportion of the total water in the chamber air, then equilibration times would be extended. Furthermore, if the kinetics of this water uptake is such that significant amounts of water are carried over from sample to sample, then serious errors in water potential determinations could result.

A variety of materials commonly used to construct chambers or as sealing gaskets were investigated with a view to assessing their relative water uptake properties. The results of this study are presented in Dixon and Grace (1982) (Appendix B). Chamber wall and gasket materials were then chosen on the basis of least water uptake and practicality, and used in the construction of the psychrometer chamber described above (Plate 4.1).

## RESULTS AND DISCUSSION

## CHAPTER 5. Experimental Determination of Heat Transfer

Aerodynamic conductance ( $g_a$ ) is a key variable in the evaluation of the effect of wind on transpiration; and, indeed, in all kinds of plant-atmosphere coupling. The effect of leaf size on  $g_a$  is well known (e.g. Gates and Papian, 1971). There is, however, no consensus on the possible roles of leaf form, turbulence and leaf proximity.

## 5.1 Effect of Leaf Form

The influence of leaf form on conductance depended on the prevailing wind regime. The smooth leaf with entire margins displayed an increase in conductance in relation to laminar 'control' conditions at a given wind speed except when the wind regime was generated by small crosspieces (Fig. 5.1(a)). When the leaf had a serrated margin the results were much the same but exhibited slightly higher conductances than the smooth leaf under similar conditions (Fig. 5.1 (b)). However, when the leaf was rippled all the turbulent regimes (i.e. those in which turbulence generating crosspieces were used) were equally effective in enhancing heat loss relative to the laminar 'control'. Also, the rippled leaf displayed, to a small extent, the highest conductances of all the leaf forms under similar conditions (Fig. 5.1(c)).

An investigation of the boundary layer of each leaf form using a Disa hot-wire anemometer revealed a turbulent boundary layer in all cases except when the smooth leaf was exposed in a laminar airstream. The power spectrum analysis showed that the turbulence frequencies produced, extended at least to 5 k Hz at a wind speed of  $5 \text{ m s}^{-1}$  (Fig. 5.2). Also, an increase in the degree of surface minutiae was associated with an increase in the signal amplitude and frequency span of

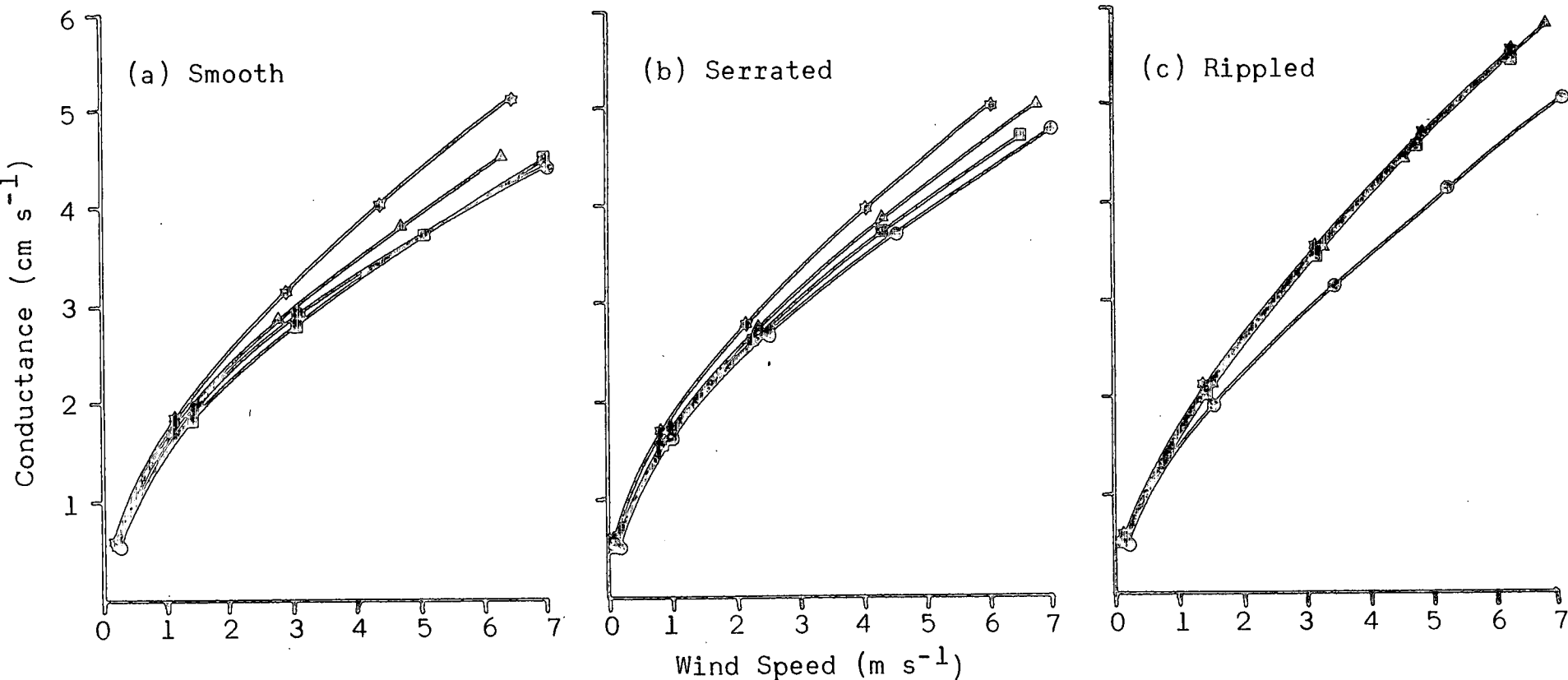


Fig.5.1 Aerodynamic conductance as a function of wind speed for three leaf types in laminar flow (○) and turbulent flow generated by small (◻), medium (△) and large (✱) crosspieces. Each point represents the mean of three determinations, reproducible to within 3%.

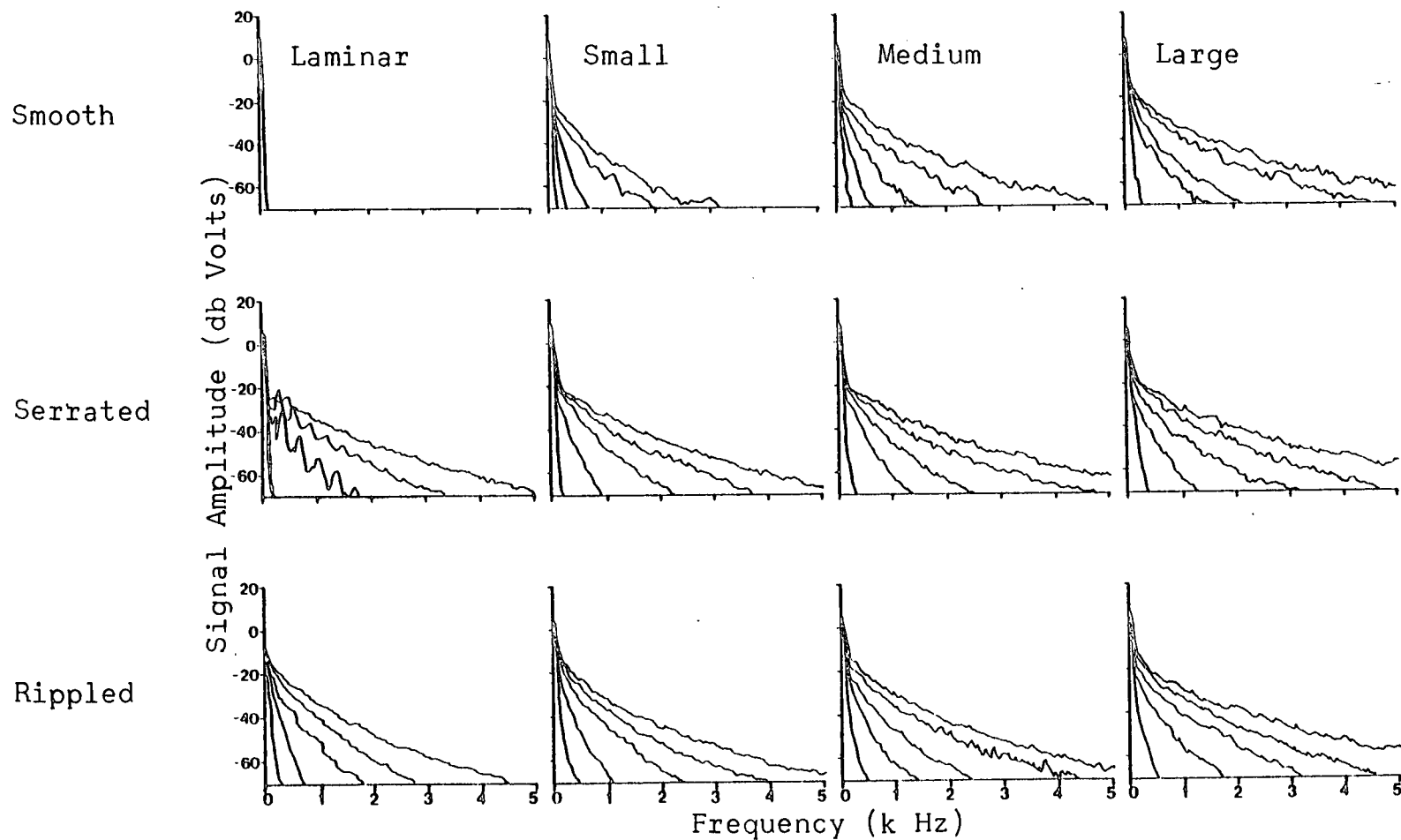


Fig.5.2 Turbulence 'signatures' taken in the boundary layers of three leaf types in laminar flow and turbulent flow generated by three sizes of cross-pieces (see text). Wind speeds of 1, 2, 3, 4 and 5 m s<sup>-1</sup> were used in each case.

turbulence. The rippled leaf produced the greatest proportions of both variables while the smooth leaf, with no surface minutiae at all, produced the least.



## 5.2 Effect of Turbulence

From the results presented in the preceding section it was apparent that the nature of the turbulent wind regime, produced either by variation in leaf form or turbulence generating crosspieces, dictated, to some degree, the extent to which conductances were enhanced.

Power spectrum analysis of the turbulence generated by the three sorts of crosspieces relative to laminar flow (Fig. 5.3) showed clearly that the large crosspieces produced the greatest amplitude and frequency span at a given wind speed. This type of wind regime consistently produced the highest conductances.

A further look at the the turbulence 'signatures' of the various leaf forms (Fig. 5.2) and corresponding conductance data (Fig. 5.1) revealed that the turbulence frequencies near 200 Hz tended to correlate best with the observed increases in conductance (Fig. 5.4). This was consistent with the observation that the highest conductances occurred with the rippled leaf and large crosspieces, conditions which produced the largest proportion of low frequency turbulence (i.e.  $\approx$  200 Hz).

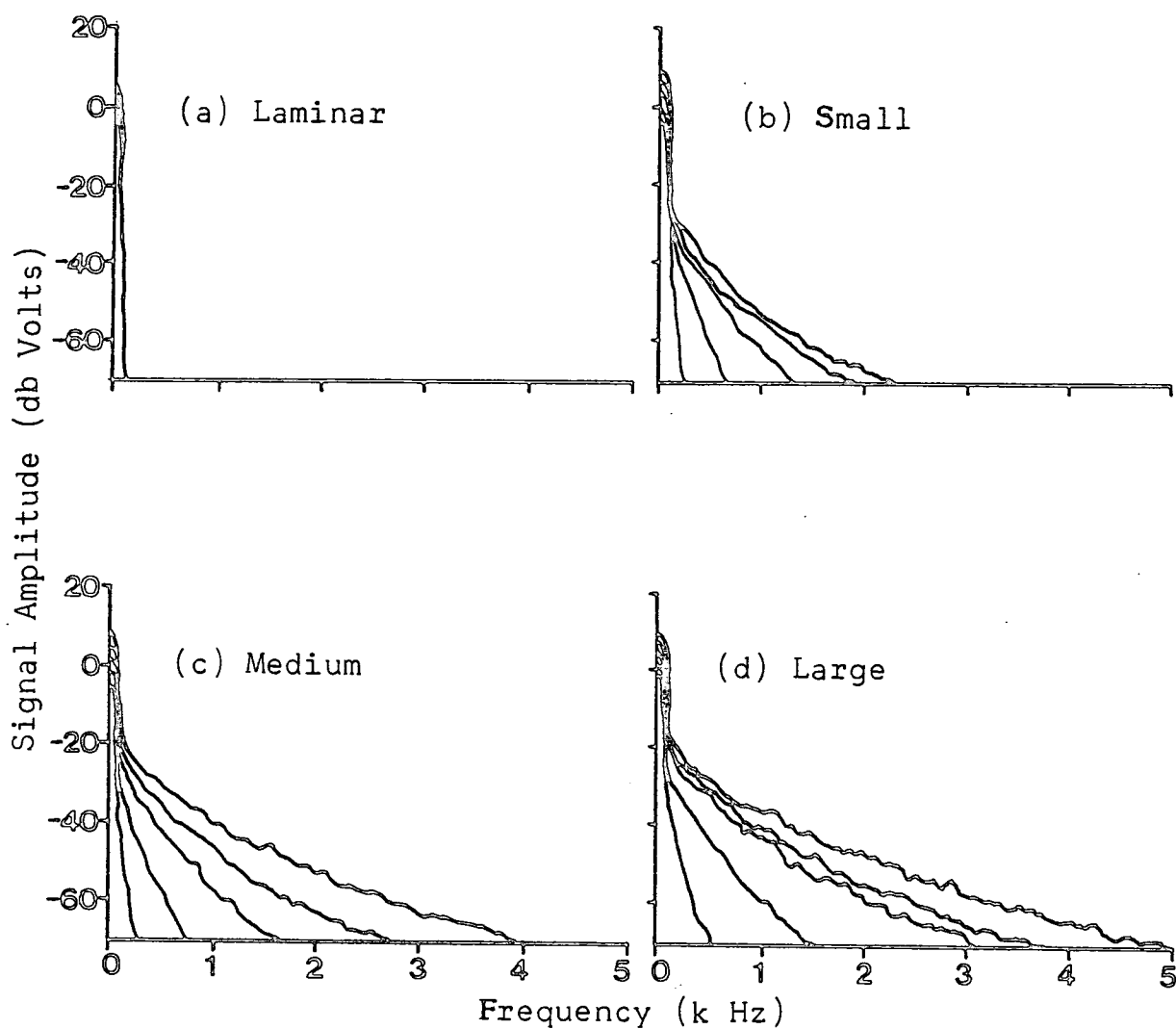


Fig.5.3 Turbulence regime in the wind tunnel with no crosspieces (a) or with various sized crosspieces (b, c, d) (see text). The five traces in graphs (b), (c) and (d) represent, from left to right, wind speeds of 1, 2, 3, 4 and 5 m s<sup>-1</sup>.

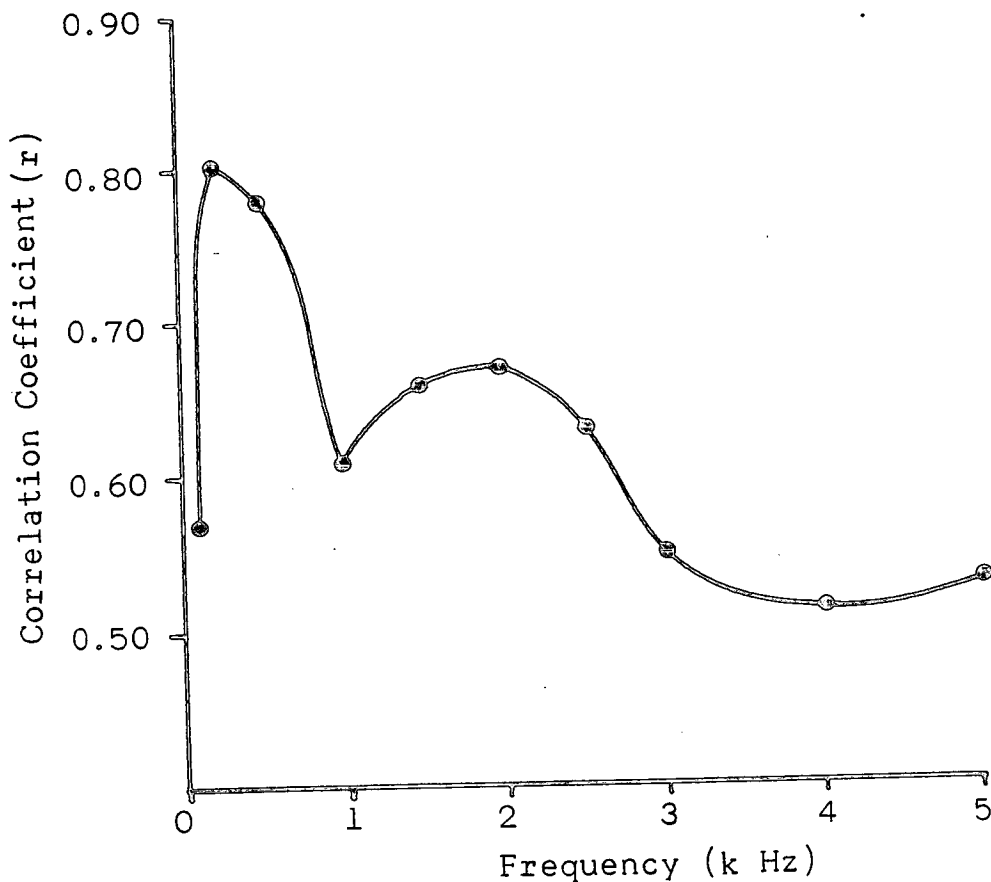


Fig.5.4 The effectiveness of different frequencies of turbulence in enhancing conductance in the three leaf types. The vertical axis is the correlation coefficient of the relationship between conductance (Fig.5.1) and signal amplitude (Fig.5.2) at various frequencies at a wind speed of  $5 \text{ m s}^{-1}$ . For ten degrees of freedom,  $r=0.57$  is significant at  $p=0.05$ . The highest wind speed ( $5 \text{ m s}^{-1}$ ) was chosen for analysis, as the range of frequency displayed was greatest at this wind speed. Other wind speeds showed similar relationships but analysis of these data sets was less reliable as the scaling factor used on the instrument's display did not permit precise extraction of data.

### 5.3 Effect of Leaf Proximity

Leaf proximity and orientation and the resultant effect on the overall shape of the plant were found to exert only minor influence on aerodynamic conductance (Fig. 5.5).

When the model leaves, which were smooth, with entire margins, were arranged parallel to wind direction in the 'swept' configuration, the conductance values followed closely those predicted by laminar boundary layer theory. The 'lax' and 'bunched' configurations (refer to Plate 3.3) displayed equal enhancement of conductance with increasing wind speed and the statistical difference from boundary layer theory was barely significant.

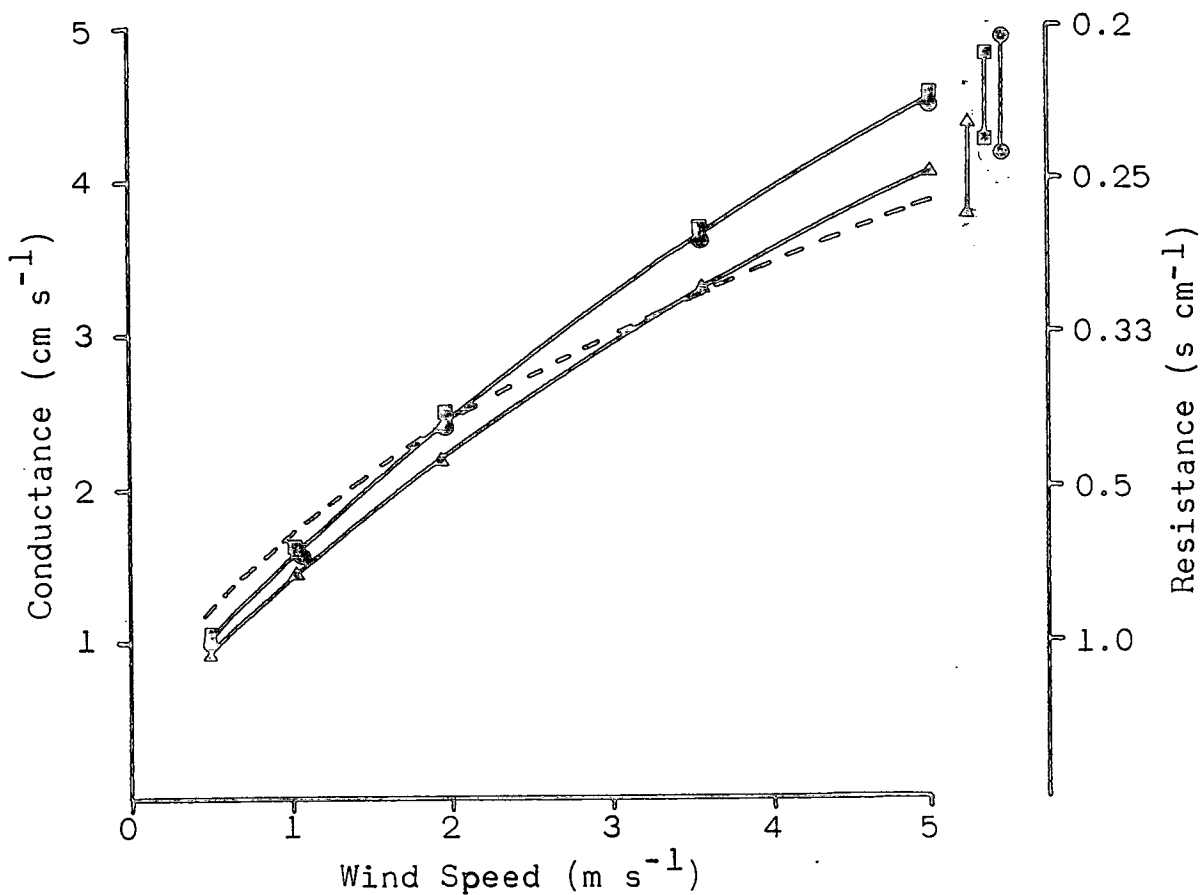


Fig.5.5 Aerodynamic conductance as a function of wind speed for three configurations of brass leaves (i.e. lax( $\odot$ ), bunched ( $\boxplus$ ) and swept ( $\triangle$ ) - see Plate 3.3). Each data point was obtained from cooling curves of ten leaves in each configuration. The error bars correspond to 95% confidence limits.

## 5.4 Comparison with Boundary Layer Theory

It is convenient when comparing exchange rates with published theory to use the Reynolds number (Re), Grashof number (Gr), and Nusselt number (Nu):

$$Re = u d / \nu \quad (5.1)$$

$$Gr = a g d^3 (T_L - T_a) / \nu^2 \quad (5.2)$$

$$Nu = d g_a / \kappa \quad (5.3)$$

where  $d$  = the characteristic dimension of the leaf (m)  
 $g_a$  = the aerodynamic conductance ( $m s^{-1}$ )  
 $u$  = the wind speed ( $m s^{-1}$ )  
 $\nu$  = the kinematic viscosity of air ( $m^2 s^{-1}$ )  
 $a$  = the coefficient of thermal expansion of air ( $^{\circ}C^{-1}$ )  
 $g$  = the acceleration due to gravity ( $m s^{-2}$ )  
 $\kappa$  = the thermal diffusivity of air ( $m^2 s^{-1}$ )  
 $(T_L - T_a)$  = the surface-to-air temperature difference ( $^{\circ}C$ )

In less mathematical terms the Reynolds number is the ratio of inertial forces (tending to disrupt unidirectional flow) and viscous forces (tending to maintain laminar flow) and is a

"convenient way of comparing the forces associated with geometrically similar bodies immersed in a moving fluid."

(Monteith, 1973)

The Nusselt number provides a basis for comparing rates of convective heat loss from similar bodies of different scale exposed to different wind speeds. The Grashof number is the ratio of the buoyancy times the inertial forces to the square of the viscous forces. A system represented by a large Grashof number experiences vigorous free convection since the buoyancy and inertial forces enhancing circulation are much greater than the viscous forces inhibiting it.

The conductance data presented in Figs. 5.1 and 5.5 expressed as Nusselt numbers (Figs. 5.6 and 5.7 respectively) agreed well with established laminar boundary layer theory.

It was noted that the slopes of the relationships between  $\log_{10} Nu$  and  $\log_{10} Re$ , relative to that calculated (0.50), tended to become steeper with increasing levels of surface minutiae (Fig. 5.6 and Table 5.1). The only case which exhibited a slope identical to that calculated from laminar boundary layer theory was the smooth leaf exposed in a laminar airstream. Reference to Fig. 5.2 showed that this case was alone in displaying virtually no turbulence. The rippled leaf showed the largest deviations in slope, even at the relatively low Reynolds numbers at which these experiments were carried out.

Conductance data from the leaf proximity experiments, which were carried out in a turbulent airstream,

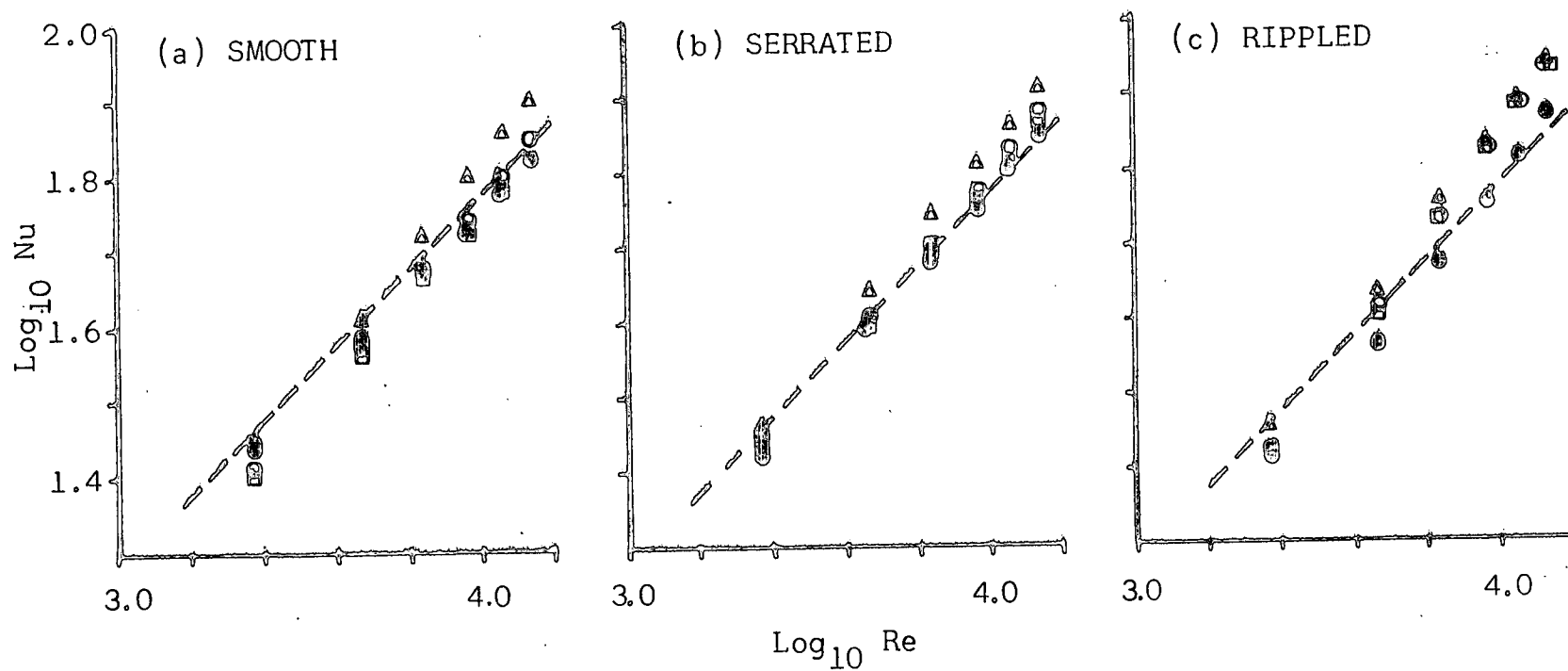


Fig.5.6 Conductances, in the three leaf forms, expressed as Nusselt numbers and plotted against the Reynolds number. Each leaf was exposed in laminar flow ( $\odot$ ) and various turbulent flows generated by three sizes of cross-pieces: small ( $\square$ ), medium ( $\circ$ ) and large ( $\triangle$ ) (see text). The broken line in each case represents this relationship calculated from boundary layer theory.



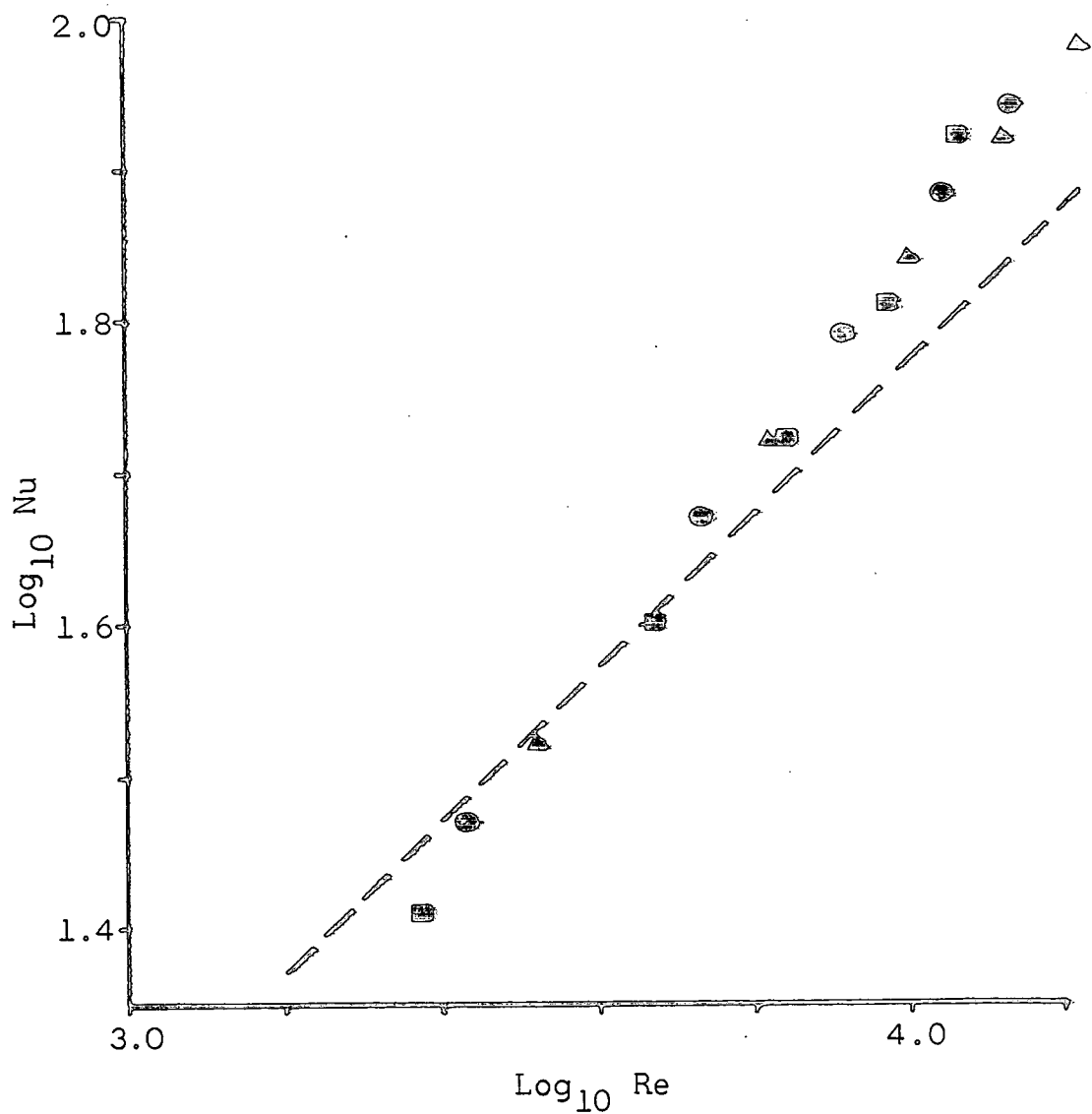


Fig.5.7 Conductances in the three configurations, lax ( $\oplus$ ), bunched ( $\boxplus$ ) and swept ( $\triangle$ ), expressed as Nusselt numbers and plotted against the Reynolds number. The broken line represents the same relationship calculated from laminar boundary layer theory.

TABLE 5.1 Slopes of the relationships between  $\log_{10} Nu$  and  $\log_{10} Re$  for each of the three leaf forms under conditions of laminar flow and three turbulent regimes. The slope of this relationship calculated from laminar boundary layer theory is 0.50.

	<u>Smooth</u>	<u>Serrated</u>	<u>Rippled</u>
<u>Laminar</u>	0.50	0.55	0.60
<u>Small</u>	0.55	0.56	0.68
<u>Medium</u>	0.57	0.55	0.67
<u>Large</u>	0.59	0.58	0.64

expressed as Nusselt numbers (Fig. 5.7) also displayed slope deviations. All of the configurations tested produced a 34% steeper slope than that of the theoretical curve.

## 5.5 Discussion

The evolutionary origins, as well as the ecological and physiological significance, of the various leaf forms observed in nature have been a subject of investigation for many years. Bailey and Sinnott (1916) raised the question as to

"whether the entire and non-entire types of (Dicotyledon) leaf-margins are determined by environmental influences, or whether they are form-variations of little functional significance that are held on by heredity?"

The results of their phytogeographical study showed an obvious correlation between leaf form and environment, a conclusion supported by Richards (1952). Both pointed out that leaves with entire margins were overwhelmingly predominant in lowland-tropical regions; those with non-entire margins in mesophytic cold-temperature areas. Bailey and Sinnott (1916) also suggest the possibility

"that the form of the leaf margin may be largely influenced, either directly or indirectly, by phenomena of evaporation and transpiration"

An evolutionary argument may call for a vice-versa point of view, however, the point is made that

since the main environmental variables involved were temperature and humidity, then the physiological significance of leaf form must be linked with transpiration. The data presented in this chapter provide a measure of the influence of non-entire leaf margins, and might be used in the future, in conjunction with the Penman-Monteith equation or an equivalent energy-balance approach, to provide answers to these questions first raised many years ago.

More recent studies have shown, quantitatively, that factors such as wave-like roughness elements, protruding veins, leaf curvature and fluttering, all contribute to some degree, to the enhancement of exchange rates of heat and mass to and from surfaces (Chamberlain, 1968; Schuepp, 1972; Grace, et al. 1980).

The nature of turbulent wind regimes and their precise role in plant-atmosphere coupling is poorly understood. Schuepp (1972) grouped fluid turbulence with other parameters causing boundary layer disturbance such as leaf curvature, surface roughness and fluttering, and expressed the difficulty in separating or determining the nature of the interactions between them. Monteith (1973) attached great importance to turbulent mixing in the layers of air over the vegetation, stating that

"without turbulence in the boundary layer, the exchange of sensible heat between the atmosphere and the surface would involve enormous diurnal

changes in temperature which plants could not endure."

He also stated that the amplitude and frequency of the velocity fluctuations in an airstream determine the point at which turbulent transition occurs but offered no data to explain this hypothesis. The relationship between such fluctuations in the velocity of the free airstream, the features of turbulence close to the leaf and the exchange rate which the leaf exhibits has never been determined and is likely to be exceedingly complex. However, many of the differences between observed and calculated exchange rates may have arisen from this complex interaction.

These differences have often been substantial. Numerous studies have been conducted where observed exchange rates have exceeded those calculated from laminar boundary layer theory. Parlange, et al. (1971) reported a decrease in aerodynamic resistance by a factor of 2.5, using tobacco leaves in a realistic turbulent wind. Pearman, et al. (1972), studying heat transfer from metal discs, observed transfer coefficients 1.5 times greater than predicted from transfer theory for laminar flow conditions. Turbulence-promoting factors on leaf surfaces were shown by Schuepp (1972) to enhance exchange rates by factors between 1.2 and 1.8. On the other hand, there were virtually no reports

to suggest that observed exchange rates may have been less than those calculated.

The discrepancies, reported in the literature, between observed and calculated exchange rates may, in some instances, have resulted from the inherent technical difficulties encountered in obtaining reliable measurements of a complex system.

The exchange rates reported here, as measured with the cooling-curve technique, agreed relatively well with established theory in most respects. This result was fortified by the reproducibility, within very fine limits, of the measured values for heat exchange from the brass leaf replicas.

The boundary layers of model leaves provided a clue to the slight discrepancies between observed and calculated conductances found here. A closer look at the turbulence characteristics of the boundary layer was required to elucidate these discrepancies. (Most authors in the past have not even attempted to characterise the turbulence in the free stream, let alone that immediately over the leaf.) Although the addition of serrations and ripples to the leaf margin caused a small enhancement of conductance, a concurrent analysis of the boundary layer assisted the interpretation of this phenomenon.

Some reports in the literature have shown the turbulent nature of leaf boundary layers. These tend to

suggest that botanical scientists have perhaps been unduly optimistic in the belief that aerodynamically complex leaves in natural flows of air should behave in the ideal manner predicted by laminar theory. Indeed, it has long been known in fluid dynamics that small wires can be used to 'trip' the air flow near a smooth flat plate, thus creating a turbulent regime (Schubauer and Skramstad, 1947). Drake, et al. (1970) reported transitions from nearly laminar to turbulent flow over leaves at a lower Reynolds number than expected from laminar theory. Grace and Wilson (1976) also showed that boundary layers over leaves were turbulent over a wide range of Reynolds number. However, it is well known that for smooth flat plates in a laminar air flow the boundary layer is truly laminar as long as the Reynolds number does not exceed  $10^5$ .

The grouping of leaves together is likely to produce at least two effects bearing on the aerodynamic boundary layer. Firstly, some degree of mutual shelter will occur, and secondly, each leaf will create a turbulent wake down-stream. These two phenomena will tend to affect heat and mass exchange oppositely and could conceivably cancel each other out. Obviously, the distance between leaves in a canopy will determine the degree to which these effects are manifested. Under free convection conditions the spacing is irrelevant to exchange rates until the individual



boundary layers actually coalesce (Schuepp, 1973). Under conditions of forced convection and turbulent transfer such factors as leaf size, position relative to wind direction and nature of the turbulent stream are likely to have some bearing on resulting exchange rates.

The conductances observed in the leaf proximity experiments indicated, from the steepness of the slope in Fig. 5.7, that convective coupling with the environment was through a turbulent, rather than a laminar, boundary layer. It is easy, qualitatively, to extrapolate this observation to consideration of a canopy of real leaves where the aerodynamic complexity must ensure turbulent conditions.

The data presented in this study confirmed the turbulent nature of the air flow over leaves, even at a low Reynolds number. Further, some progress was made towards defining the turbulence types associated with specific exchange rates in the artificial system studied.

## CHAPTER 6. The Effect of Wind on Transpiration

The effect of wind on transpiration was examined both theoretically, using the Penman-Monteith equation, and experimentally, by subjecting plants to different wind speeds in a controlled environment wind tunnel. In the first part of this chapter the Penman-Monteith equation is used to explore the influence of some of the environmental and physiological variables on calculated transpiration. Next, experimental results in more-or-less well defined environmental conditions are presented and compared with the theoretical predictions. Finally, an attempt is made to reconcile the calculated and observed results and a sensitivity analysis is carried out to discover whether the discrepancies can be accounted for by the uncertainty in the environmental parameters.

## 6.1 A Note on Resistances versus Conductances

There is no consensus as to whether resistance or its reciprocal, conductance, should be used in the analysis of diffusion pathways. In the present work, conductance has been used when attention has been focussed on the effect of variables (e.g. wind) on heat loss from a brass leaf, as conductances are simply proportional to heat losses. However, when stomatal and aerodynamic components are to be considered together it seems appropriate to use resistances, as the diffusion pathway, consisting of resistances in series, is simply considered in terms of the sum of the component resistances.

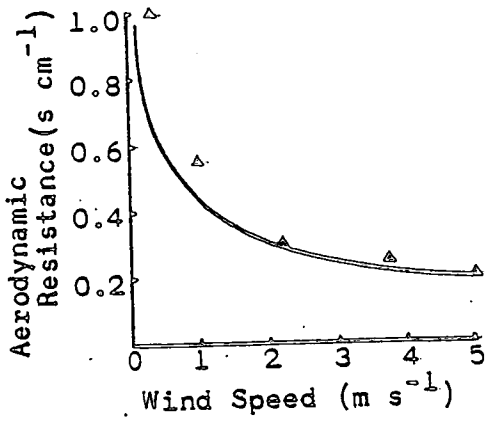
## 6.2 Calculated Rates of Transpiration

The form of the Penman-Monteith equation presented in Chapter 1 (Equation (1.7)) was used in the Fortran computer program, PENTEITH (Appendix C) to predict transpiration rates under conditions of many different values of net radiation ( $R_n$ ), saturation vapour pressure deficit (SVPD), characteristic dimension( $d$ ), wind speed ( $u$ ) and stomatal resistance ( $r_s$ ). In order to use this equation in a predictive sense, a relationship between wind speed and aerodynamic resistance must be assumed. As described in Chapter 3, an experiment was carried out in which, for each species under test, one of the leaves was replaced with a polished brass leaf so that  $r_a$  could be determined as a function of wind speed. The result (Fig. 6.1) supports the use of the standard relationship calculated from laminar boundary layer theory which allows the calculation of  $r_a$  from a knowledge of wind speed and characteristic dimension using the formula:

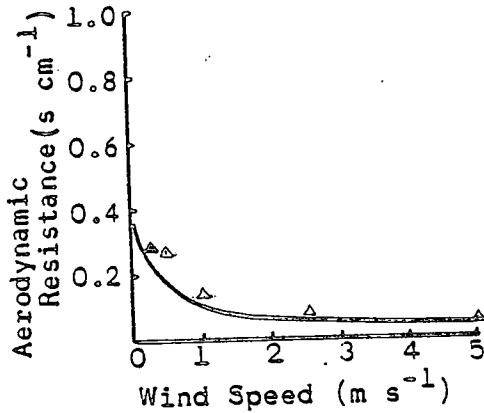
$$r_a = \frac{d^{0.5} \nu^{0.17}}{0.66D^{0.67}u^{0.5}}$$

where  $\nu$  = kinematic viscosity of air ( $\text{m}^2\text{s}^{-1}$ )  
 $D$  = diffusion coefficient of water vapour  
in air ( $\text{m}^2\text{s}^{-1}$ )

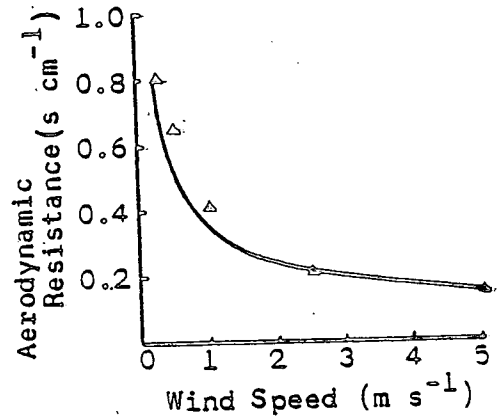
Rhododendron ponticum



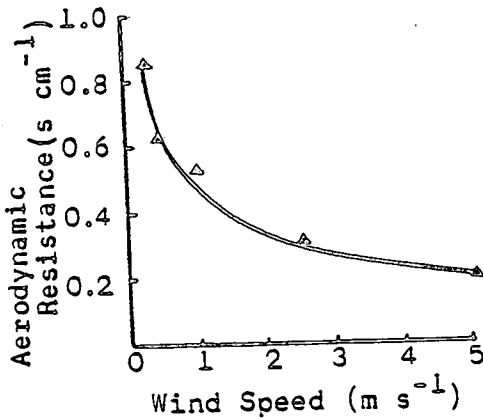
Pinus sylvestris



Sorbus aucuparia



Quercus robur



Fagus sylvatica

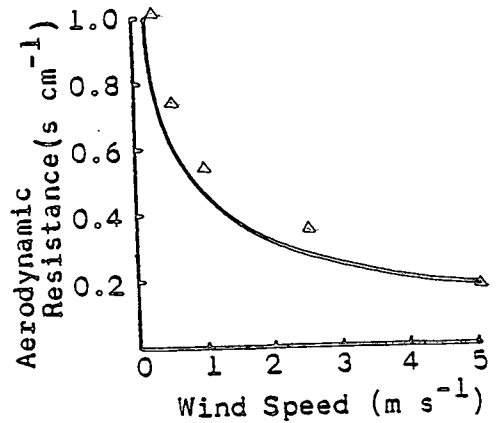


Fig.6.1 The effect of wind speed on  $r_a$  found by calculation (solid line, see text) and measured (  $\Delta$  ) using the cooling curve technique of Grace, Fasehun & Dixon (1980).

This relationship having been established and inserted, along with the Penman-Monteith equation, into the computer program mentioned above, the transpiration rate was calculated over much of the range of each variable normally encountered in the field. The results, part of which are shown in Fig. 6.2, predicted that an increase in wind speed would cause a decline in transpiration rate in many conditions except for the lowest level of available energy.

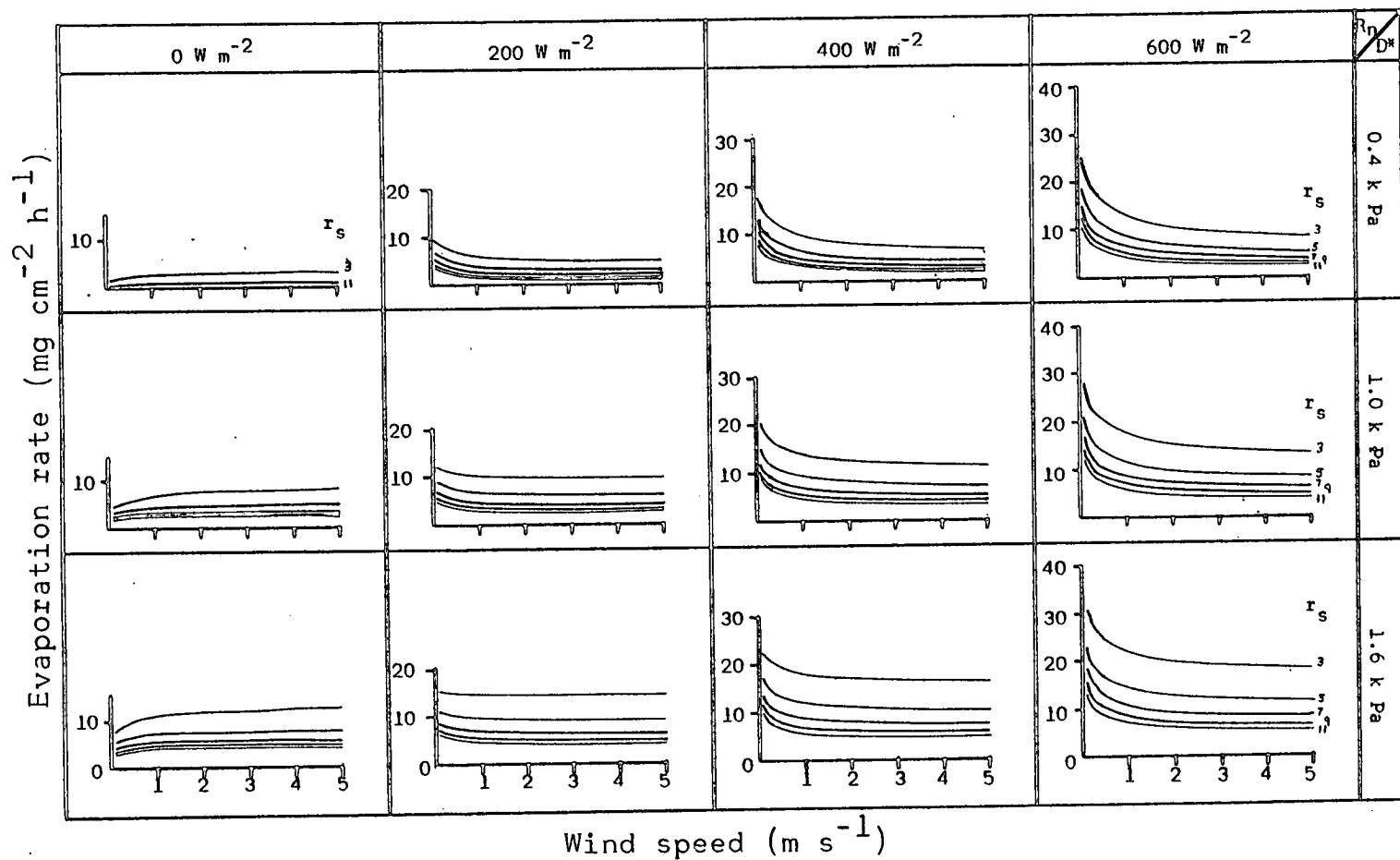


Fig.6.2 The calculated effect of wind speed on the water loss from leaves with a characteristic dimension ( $d$ ) of 2.1 cm at four levels of available energy ( $R_n$ ) (0, 200, 400, &  $600 \text{ W m}^{-2}$ ), three levels of saturation vapour pressure deficit ( $D^*=SVPD$ ) (0.4, 1.0, & 1.6 kPa) and five values of stomatal resistance ( $r_s$ ) (3, 5, 7, 9, & 11  $\text{s cm}^{-1}$ ). The rates of water loss apply to individual leaves exposed at the conditions stated, and are expressed on a plan area basis.

### 6.3 Observed Rates of Transpiration

Transpiration rates usually fell in response to an increase in wind speed (Figs. 6.3-6.7). Increasing wind speed always decreased  $r_a$  and the leaf-air temperature difference. In all cases except P. sylvestris (Fig. 6.4) a concurrent reduction in leaf-air vapour pressure difference was observed. P. sylvestris exhibited the least leaf-air temperature differential, and the anomolous VPD changes observed in that species were dominated by inherent inadequacies in environmental control rather than by the changes in leaf temperature.

The decline in transpiration generally observed was qualitatively similar to that predicted by the Penman-Monteith equation under the conditions which prevailed in each experiment (Fig 6.8). Possible explanations for the apparent discrepancies in some of the cases will be discussed later.

#### 6.3.1 Observed Stomatal Resistances ( $r_s$ )

There were measurable effects of wind on stomatal resistance in some cases (Figs. 6.4-6.7). In Q. robur and S. aucuparia the stomatal resistance decreased as wind speed increased. This decline resembled the decline in VPD and may reflect the influence of VPD on stomata (see Whitehead and Jarvis, (1981), for a review of



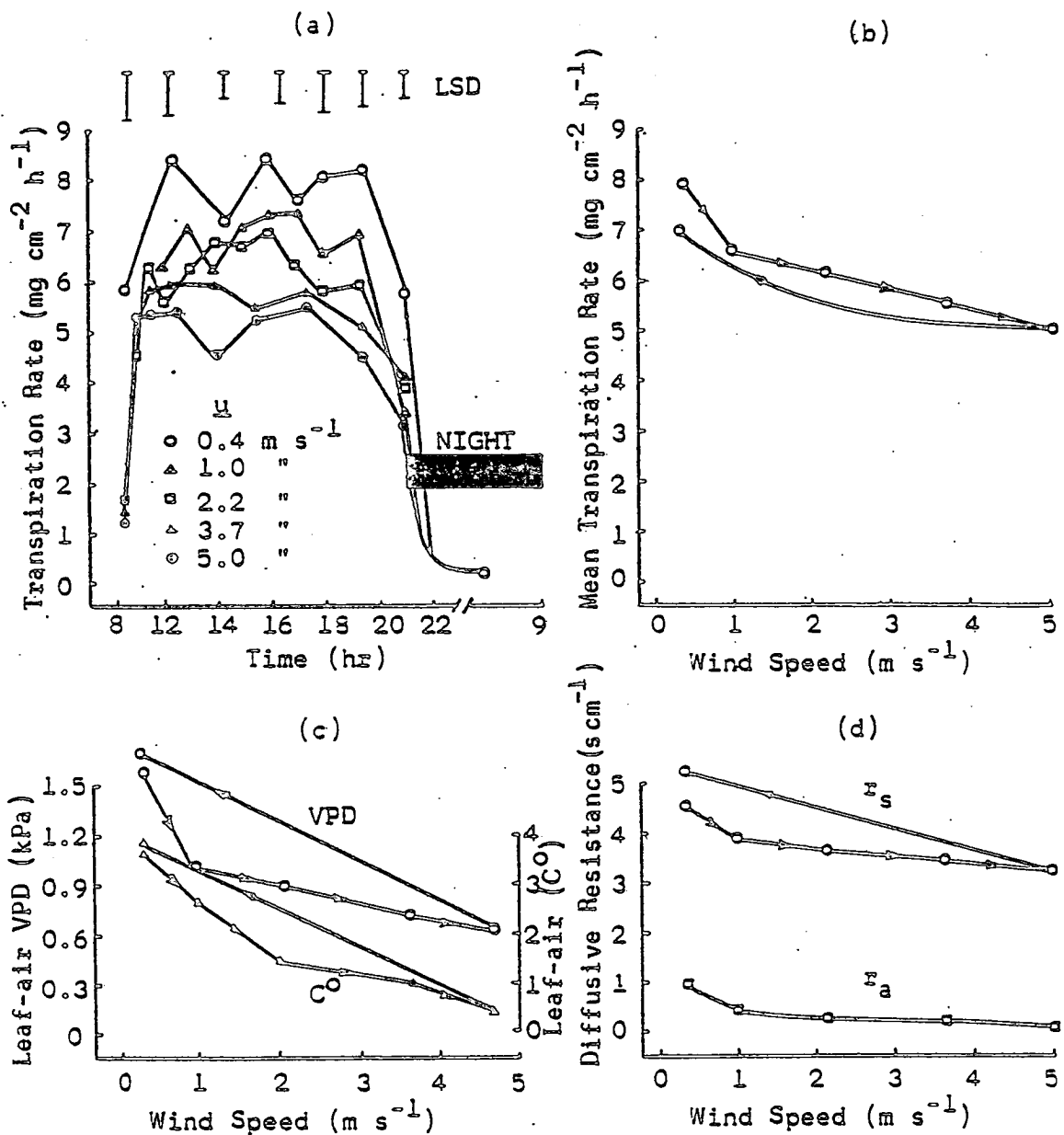


Fig.6.3 Rhododendron ponticum. The effect of wind speed on transpiration rate (a & b), the temperature difference between leaf and air (c), the vapour pressure difference between leaf and air (c), and the stomatal ( $r_s$ ) and aerodynamic ( $r_a$ ) components of diffusive resistance (d).

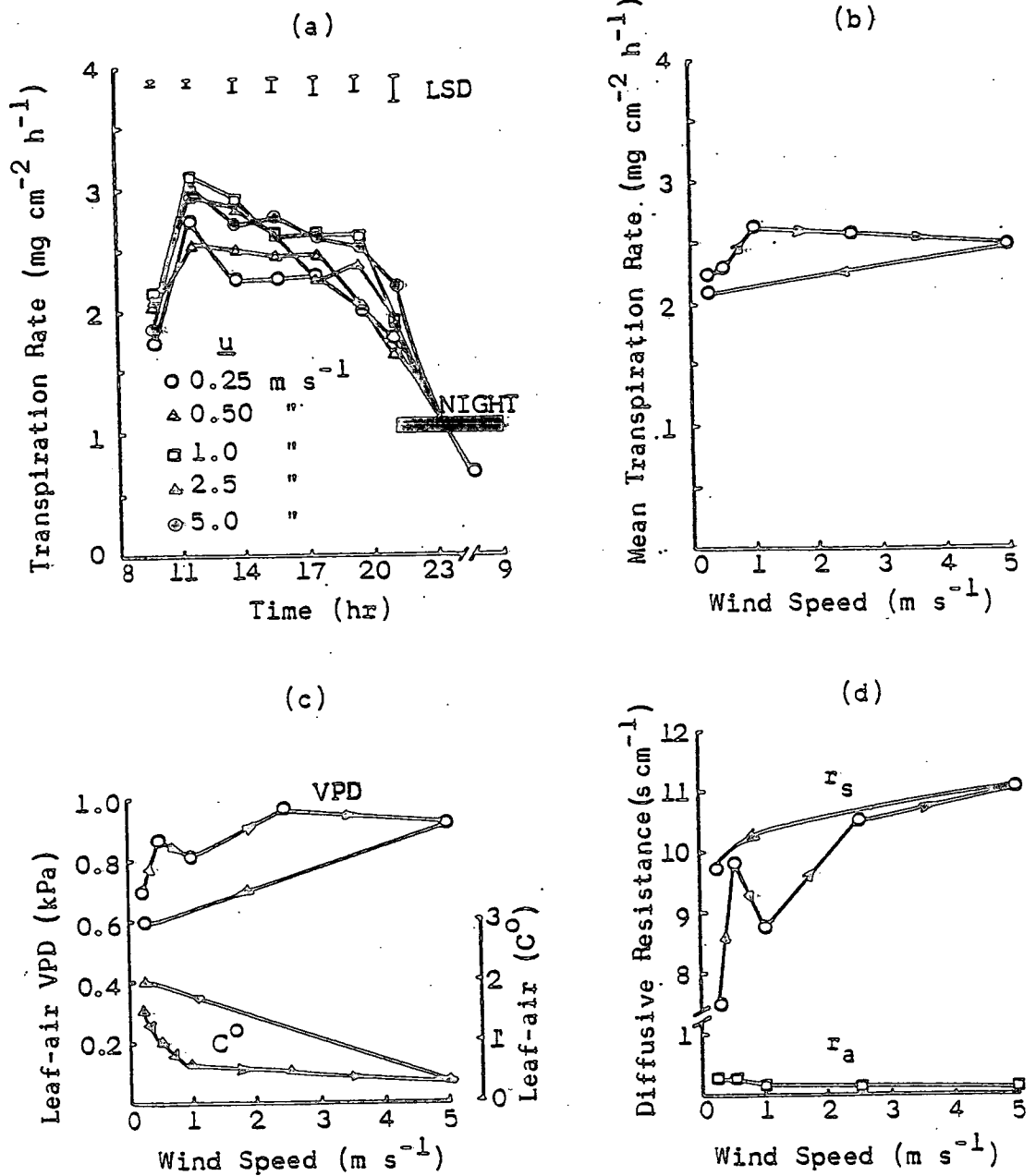


Fig.6.4 Pinus sylvestris. The effect of wind speed on transpiration rate (a & b), the temperature difference between leaf and air (c), the vapour pressure difference between leaf and air (c), and the stomatal ( $r_s$ ) and aerodynamic ( $r_a$ ) components of diffusive resistance (d).

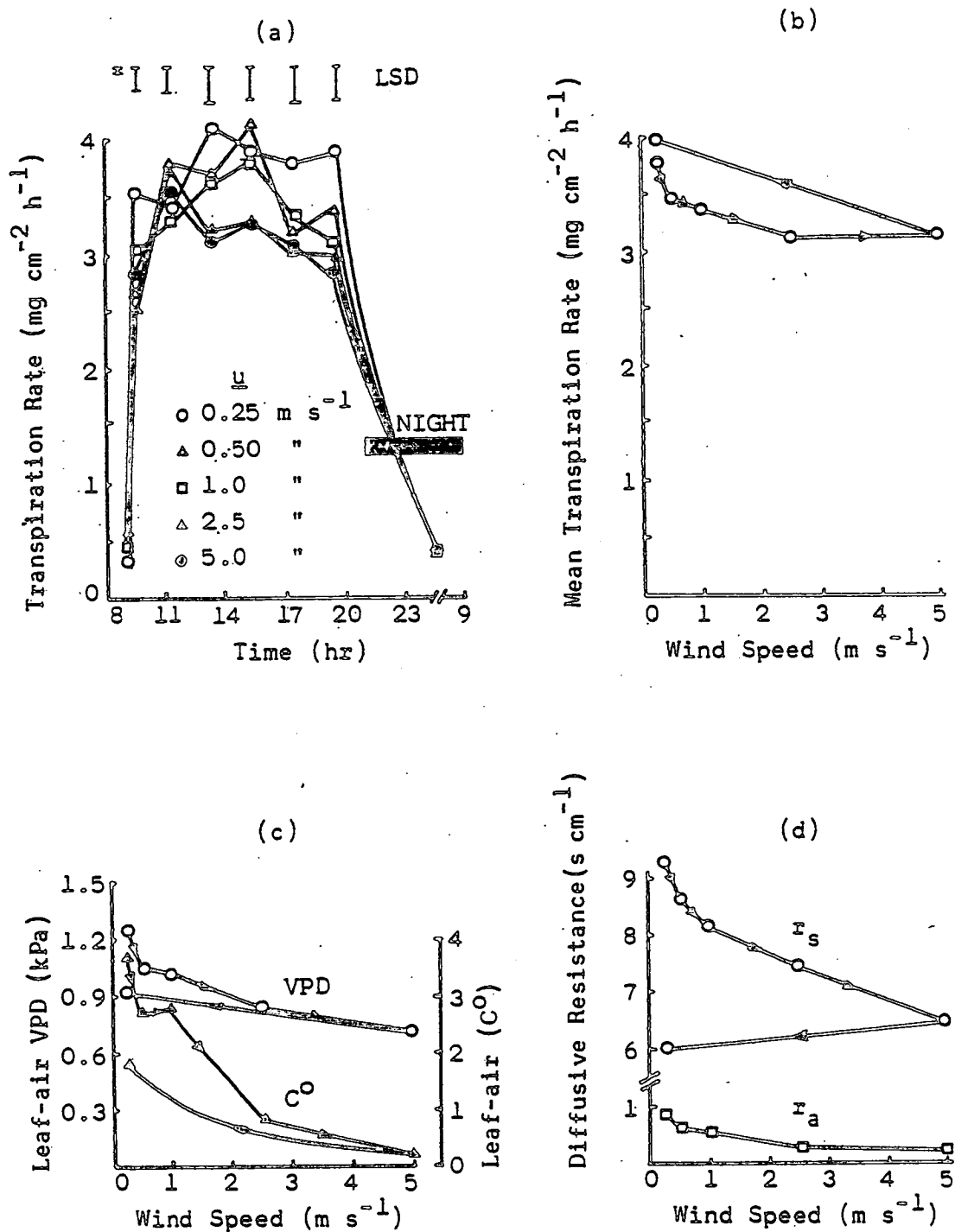


Fig.6.5 *Quercus robur*. The effect of wind speed on transpiration rate (a & b), the temperature difference between leaf and air (c), the vapour pressure difference between leaf and air (c), and the stomatal ( $r_s$ ) and aerodynamic ( $r_a$ ) components of diffusive resistance (d).

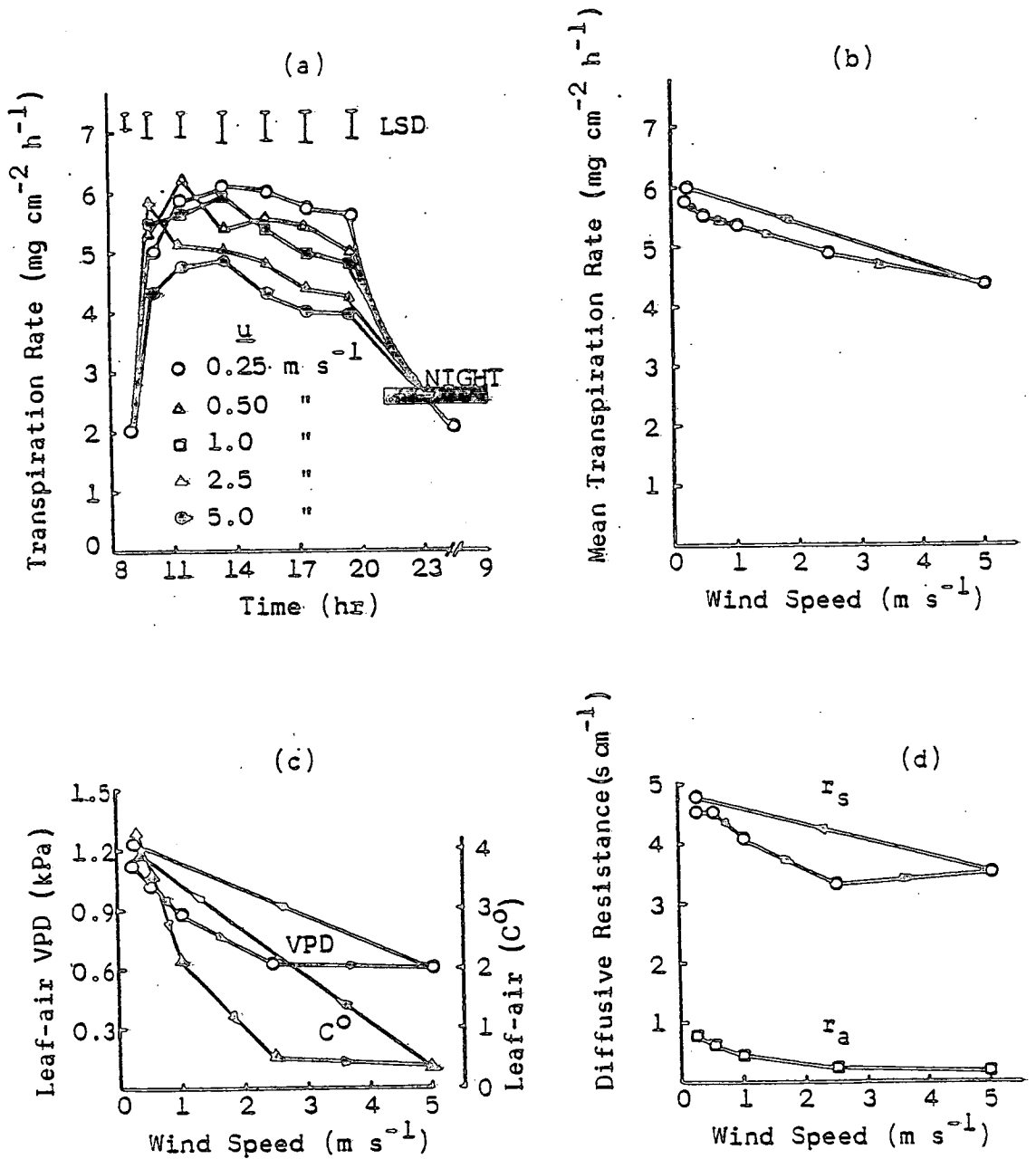


Fig.6.6 *Sorbus aucuparia*: The effect of wind speed on transpiration rate (a & b), the temperature difference between leaf and air (c), the vapour pressure difference between leaf and air (c), and the stomatal ( $r_s$ ) and aerodynamic ( $r_a$ ) components of diffusive resistance (d).

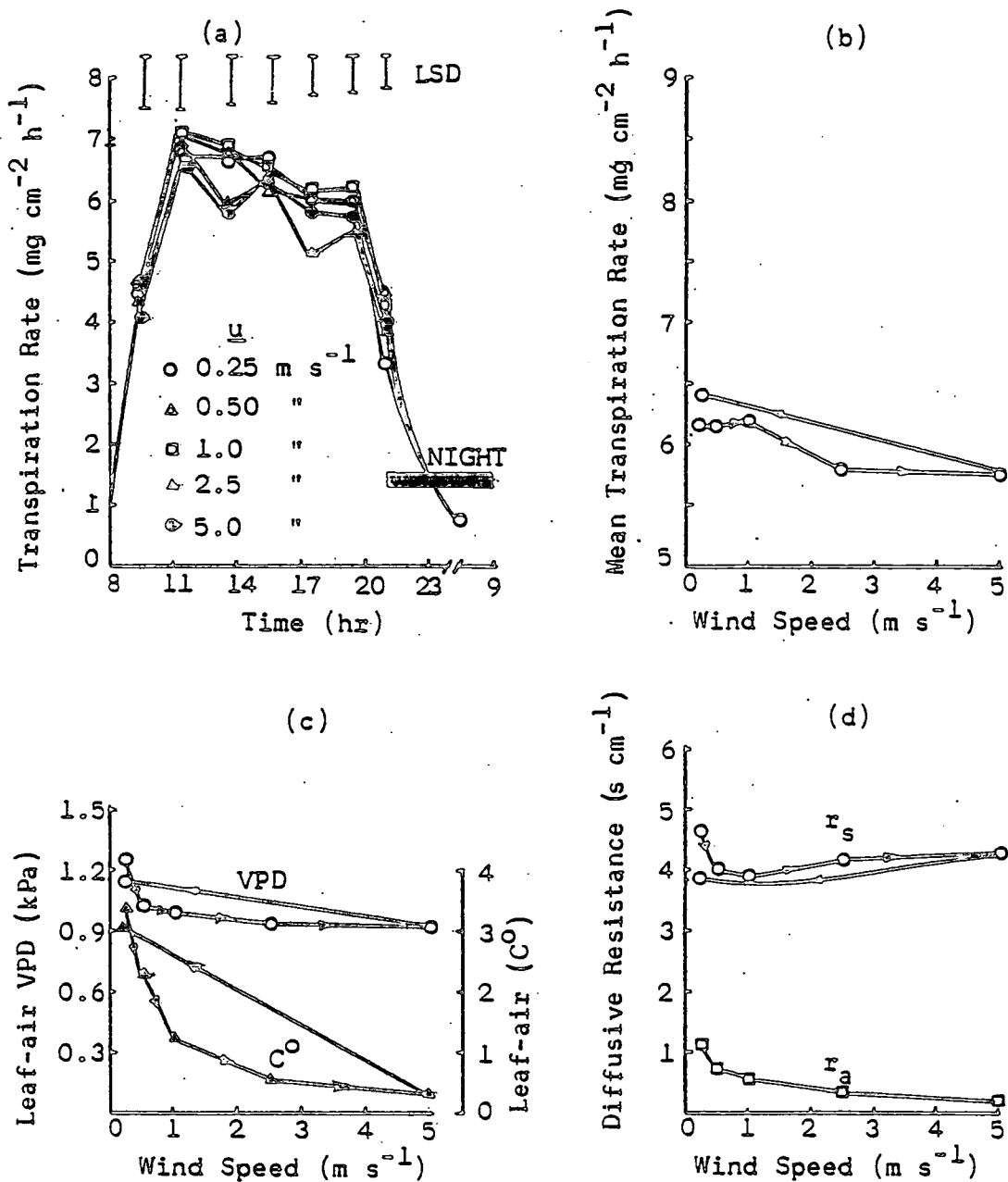
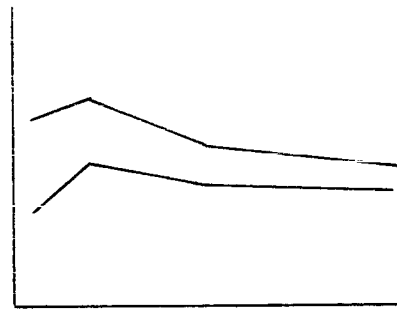
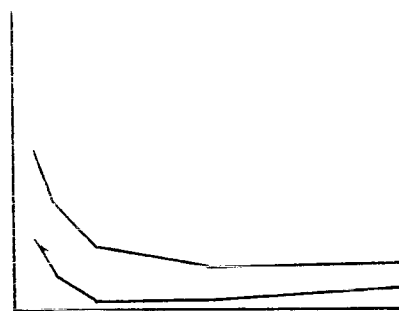
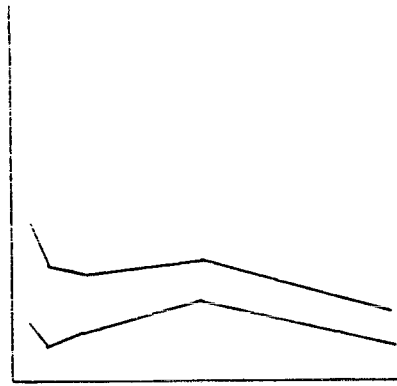
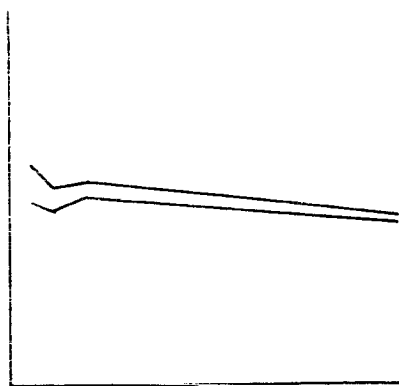
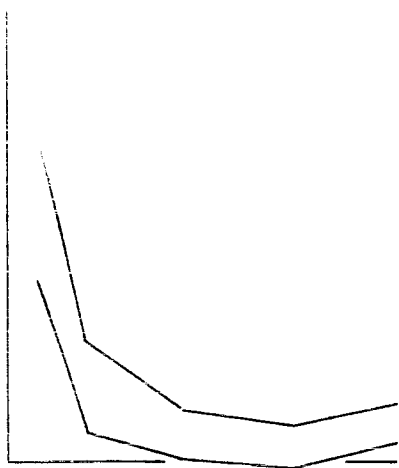


Fig.6.7 *Fagus sylvatica*. The effect of wind speed on transpiration rate (a & b), the temperature difference between leaf and air (c), the vapour pressure difference between leaf and air (c), and the stomatal ( $r_s$ ) and aerodynamic ( $r_a$ ) components of diffusive resistance (d).



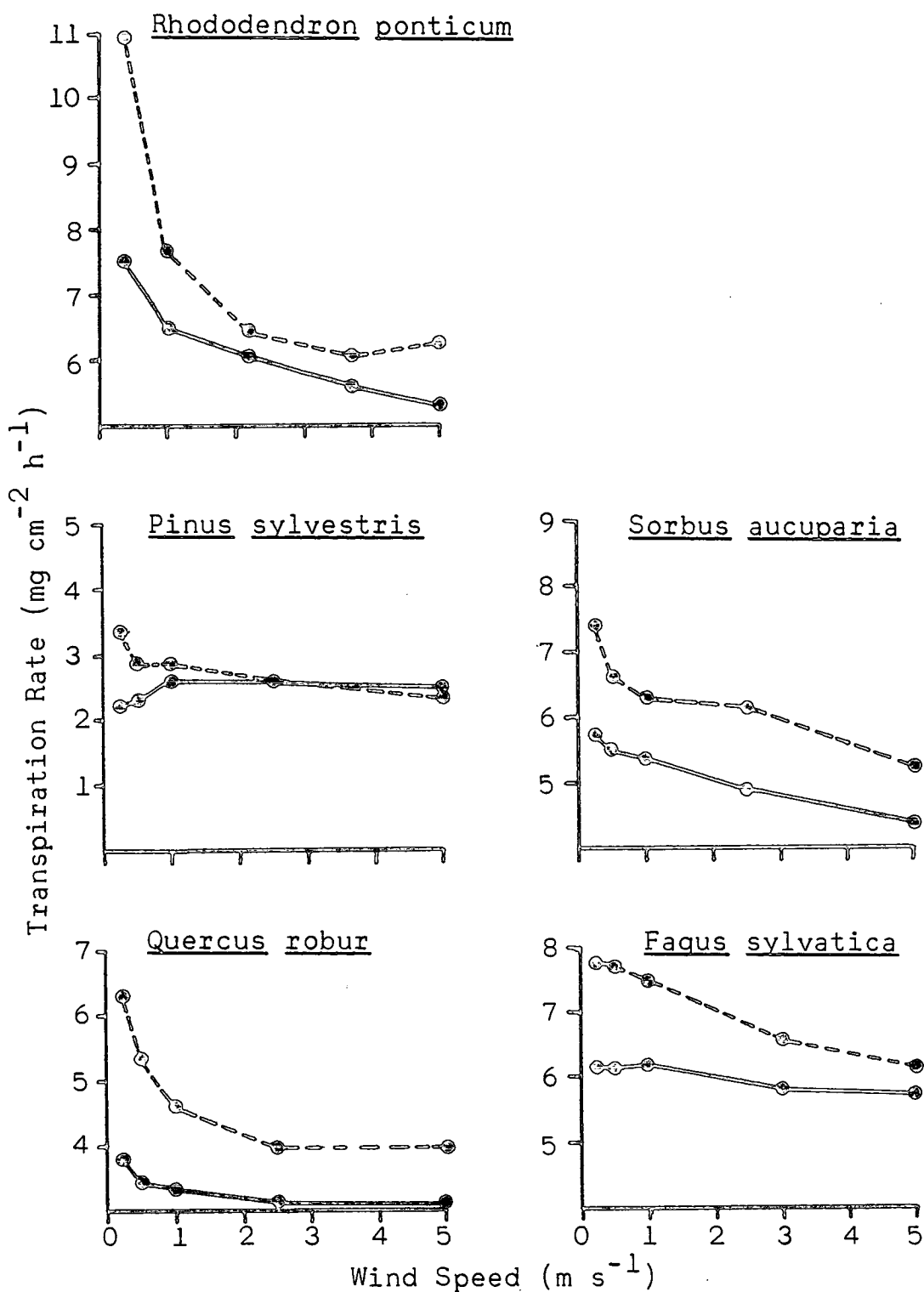


Fig.6.8 Comparison between measured transpiration rates (solid line) and those calculated (dotted line) using the Penman-Monteith equation. The overlay shows ranges of calculated transpiration rates based on corrected  $R_n$  values suggested in Appendix D. (Note the variable zero offsets of the transpiration rate axes.)

this phenomenon). In P. sylvestris, on the other hand, the stomatal resistance increased with wind speed indicating some degree of stomatal closure.

When the wind speed was returned to its lowest setting the stomatal resistance was often restored to near its original value. This lack of hysteresis indicated that damage to the leaf surface by wind action, which would have decreased cuticular resistance, was not very significant in these species. However, the data for Q. robur did show hysteresis in  $r_s$  (Fig. 6.5) perhaps suggesting a degree of cuticular damage or some not readily reversible stomatal opening in wind. The hysteresis in P. sylvestris was in the opposite direction (Fig. 6.4) and suggests that the partial stomatal closure apparent at the high wind speed was not reversed when calm conditions were restored.

#### 6.3.2 Observed Rates of Night-Time Transpiration

Transpiration in the dark was averaged over the period one-half hour after the lights went out to one-half hour before they came on. The thick-cuticled species of R. ponticum and P. sylvestris maintained relatively low and steady rates of night-time water loss with increasing wind speed while the softer, broad-leaved species displayed irreversible increases (Fig. 6.9).



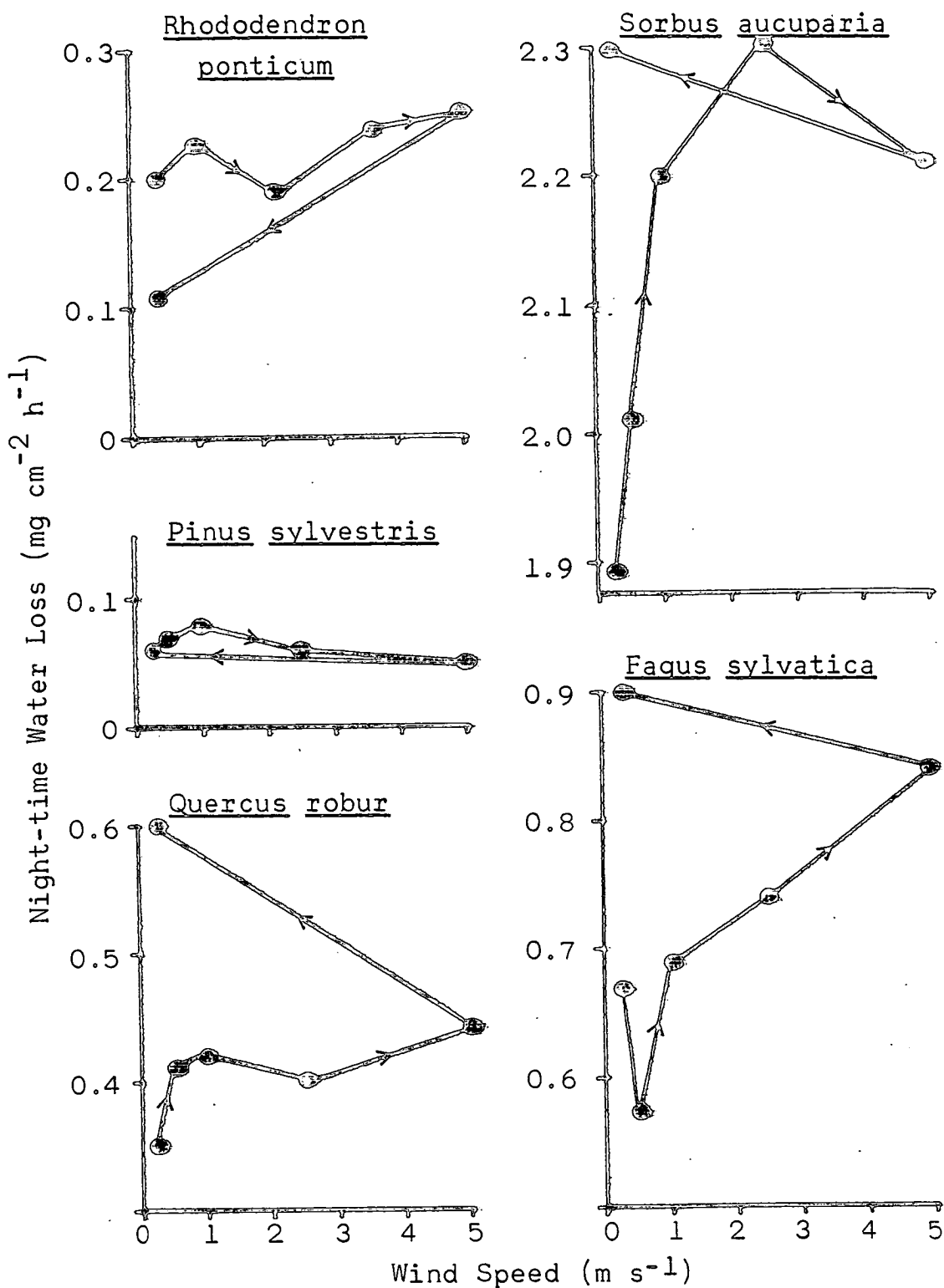


Fig.6.9 Water loss in the dark, for the five species studied, as a function of increasing wind speed. Note the variable zero offsets of the vertical axes.

#### 6.4 Components of Water Potential

Total water potential in *P. sylvestris* followed a typical diurnal pattern with the highest potential being recorded at the beginning of the photoperiod and the lowest towards the end of the day (Fig. 6.10). The data show that the plants were only mildly stressed, as intended. An increase in wind speed tended to decrease total water potential and osmotic potential. The net effect in terms of turgor potential was that the changes in osmotic potential offset the decrease in total potential, resulting in a maintenance of the status quo.

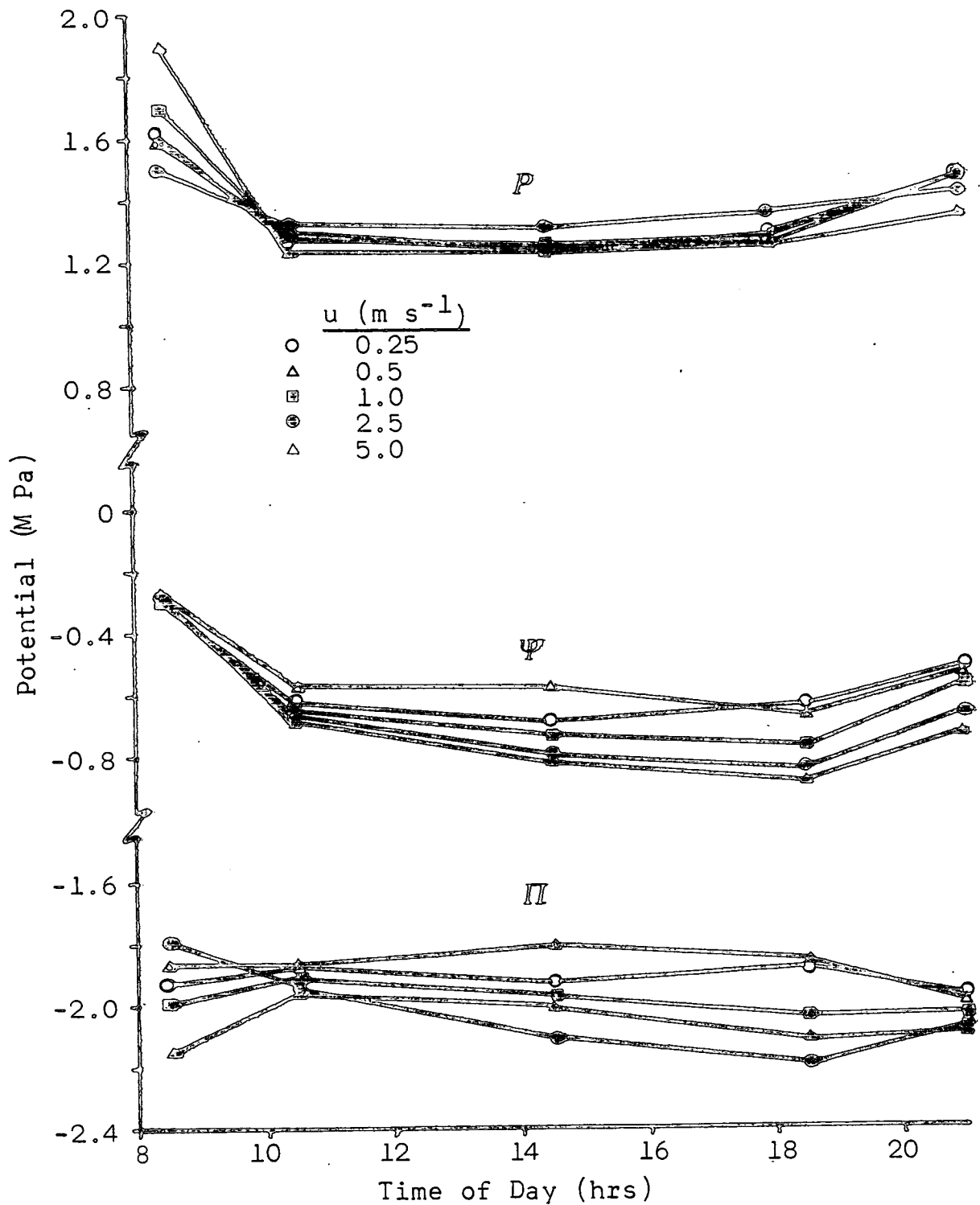


Fig.6.10 Measurements on Pinus sylvestris throughout the day, under conditions of daily increasing wind speed, of osmotic potential ( $\Pi$ ), total water potential ( $\Psi$ ), and turgor potential ( $P$ ) calculated by mean difference. Tests of statistical significance using two-way analysis of variance: both  $\Psi$  and  $\Pi$  were significantly affected by wind speed ( $p < 0.01$ ). There was no significant effect on  $P$ .

## 6.5 Discussion

### 6.5.1 Wind and Transpiration

The rate of transpiration from the leaves of plants like those studied here should be proportional to the driving force, which is the water vapour pressure difference between substomatal cavities and the air, provided the diffusion resistances in the leaf and boundary layer remain constant. The data presented above tend to show that this was substantially true, under the experimental conditions considered, after the interactions of the various physical and physiological factors were considered. Most of the effects of wind on transpiration could be explained in terms of the influence of wind on leaf temperature, and hence on vapour pressure in the substomatal cavity. However, apart from this consideration, other factors, such as changes in the physiological resistance ( $r_s$ ) and damage to the leaf surface, also come into play. Consideration of these factors provokes agreement with Grace (1981) that

"the influence of wind on transpiration may be very complex."

Previous studies concerned with wind and transpiration, or some factors affecting transpiration,

have reported widely variable and often conflicting results. Daubenmire (1959), in a well known text book, stated that

"wind increases transpiration by removing layers of humid air which tend to accumulate adjacent to the plant surfaces."

Marshall (1967), in his review, claimed that decreased transpiration in sheltered areas allows conservation of soil moisture. The aspect of shelter, and therefore of wind, and its effect on water loss has received much attention in the literature. Some reports have shown transpiration decreasing in shelter (Skidmore and Hagen, 1970; Frank and Willis, 1972) while others have shown the reverse (Rosenberg, 1966; Skidmore, et al. 1972).

Tranquillini (1969) reported that transpiration in Larix decidua and Alnus viridus increased with increasing wind speed up to 4 and 10 m s<sup>-1</sup> respectively, while Rhododendron displayed a sharp decrease beginning at low wind speed. Grace (1974) showed that the transpiration of Festuca arundinacea increased with wind speed, although in this case damage to the leaf surface was shown. In a more theoretical approach, Monteith (1965), Linacre (1964) and Campbell (1977) were unanimous in the view that increasing wind speed decreased transpiration by lowering leaf temperature

and thereby lowering the vapour pressure difference between leaf and air. This was demonstrated experimentally by Satoo (1951 a, b, c), Mellor, et al. (1964) and Drake, et al. (1970).

The apparent inconsistency in the literature seemed confounded by a more important consideration, that of determining a mechanism to explain the observed results. A consensus in this respect was even more elusive due to the variety of factors involved, both physical and physiological, which include stomatal resistance, aerodynamic resistance, water vapour pressure, leaf temperature, air temperature and soil moisture.

According to van Eimern, et al. (1964) the

"greater soil moisture in the wind sheltered area can in most cases be seen as the main reason for better crops there."

However, Rosenberg (1966) reported less soil moisture in sheltered areas which he attributed to lower stomatal resistance and increased transpiration resulting in a more rapid depletion of soil water in these areas of lower wind speed. This interpretation of Rosenberg's (1966) results suggested a physiological control via stomatal aperture, of transpiration. However, Mellor, et al. (1964) concluded that

"with few exceptions, the behaviour of the leaf in our experiments can be explained on the basis of purely physical reactions."

The exceptions they referred to were the physiological adaptations apparent only at unnaturally high radiation levels and wind velocities.

The plethora of experimental data supporting one mechanism or another, physical or physiological, tends to suggest that either some of the investigations omitted to record or report crucial parameters or the true mechanism explaining the effects of wind on transpiration is a complex interaction of all the factors involved. Certainly, the often impractical or technically difficult task of obtaining reliable estimates of all key variables in various experimental situations can be seen to cloud interpretations. Many of the earlier workers have omitted even to attempt to control or measure two of the most important variables, net radiation and absolute humidity.

Yet another variable which has escaped consideration in many cases is the role of the cuticle in the transpiration path. Grace (1974) and Thompson (1974) showed that the observed increases in transpiration with increasing wind speed in Festuca were due to increased cuticular conductance as a result of abrasive damage. That this phenomenon of surface damage occurs was upheld by MacKerron (1976) in a study of damage to

strawberry leaves. Wilson (1978) also showed abrasive leaf damage in response to wind. There are interesting differences between species in the time taken for this damage to reach a maximum. In Festuca the maximum damage was achieved in a day or so (Grace, 1974) whereas in Acer it took about 10 days (Wilson, 1978). Clearly, some plant surfaces are more durable than others, and many are completely resistant to damage. Moreover, some leaves flutter and collide more readily than others.

The species reported on in this study displayed a variety of quantitative changes in night-time transpiration in response to increasing wind speed. As expected, the heavier cuticled test species had the lowest rates of water loss in the dark when the stomatal resistance would have been greatest. Furthermore, they exhibited the least response, in terms of night-time transpiration increases, to increasing wind speed. On the other hand, night-time water loss in the softer cuticled species showed irreversible increases, in the short term, as well as inter-specific variations in the values of these rates of water loss. The three species of this classification each displayed a higher rate of day-time transpiration when returned to the calmest conditions than was recorded before they were subjected to daily increases in wind speed. This suggested possible cuticular damage leading to increased cuticular transpiration or a degree of stomatal opening



in the dark which was induced by high winds. In some cases the magnitude of the night-time flux is so large that it is almost certain that the stomata did not properly close (e.g. S.aucuparia, Fig. 6.9).

Further interpretation of these results was confounded by the unknown relative contributions of stomatal and cuticular transpiration and the inter-specific differences in the response to wind of these two variables.

#### 6.5.2 Evaluation of Experimental Conditions

The present study concerned the evaluation of the effects of wind on the transpiration of five different species. Conditions in the wind tunnel were roughly representative of outdoor, north temperate climates in the summer, though limited to some extent by the design of the wind tunnel and its associated control system.

The first important limitation here was that net radiation varied somewhat over the course of a day and between days (e.g. Fig. 6.11). This is because the long wave downward component is a function of the surface temperature of the glass ceiling, which warms up over the first few hours of the day and equilibrates at a temperature which depends on the wind speed to some extent. Fundamental reconstruction of the wind tunnel

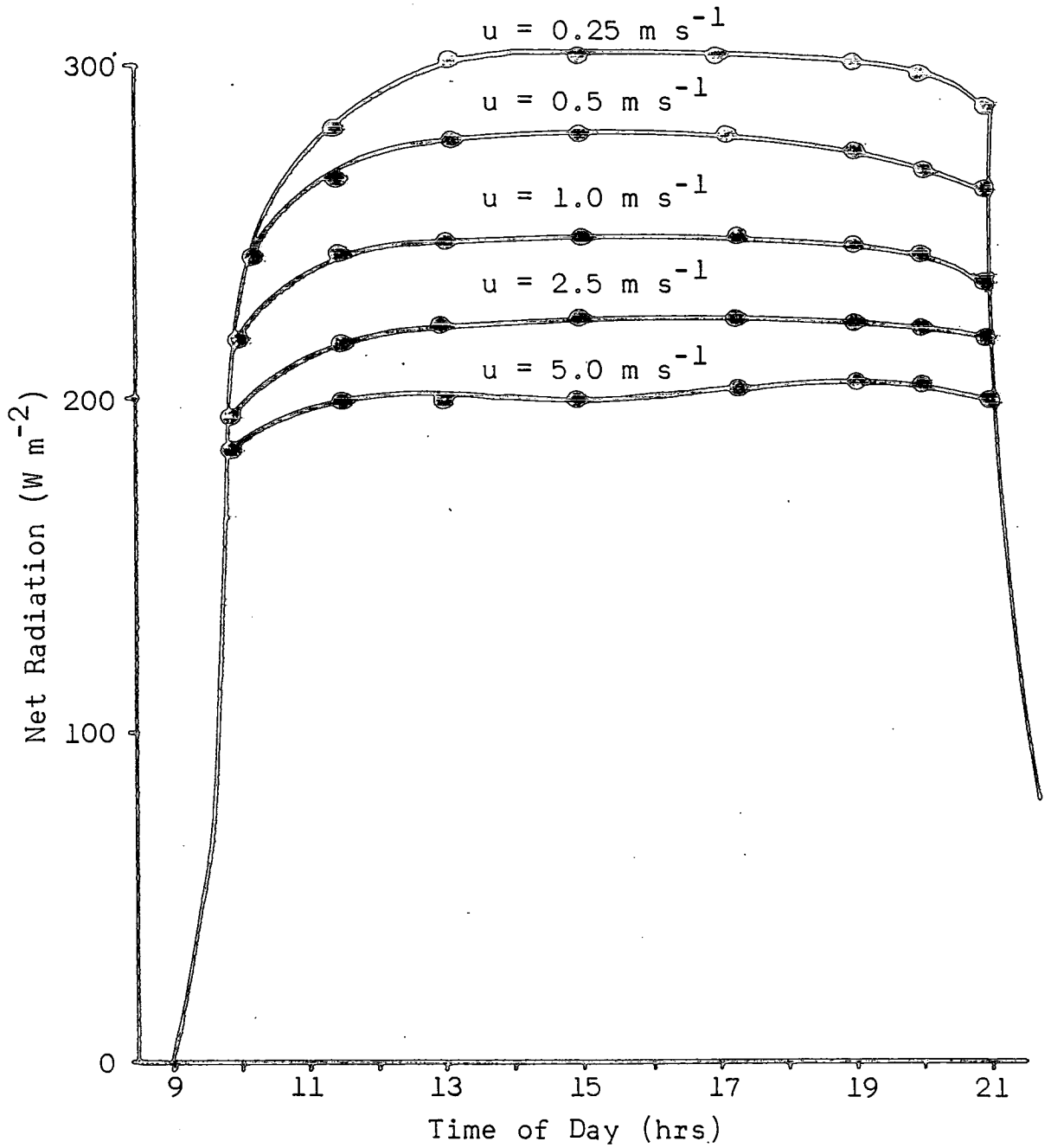


Fig.6.11 Observed net radiation changes in a Quercus robur seedling canopy as a function of time of day and wind speed ( $u$ ).

would have been required to overcome such difficulties. Moreover, even if the wind tunnel design was perfect, and created a completely constant radiation environment, the temperature variation of the leaf surface would, itself, cause some variation in the value of net radiation.

Another important limitation was that humidity control in the closed system wind tunnel used was best at high wind velocities and periodic fluctuations ( $\pm 2$  mb) occurred at the lower wind speeds.

#### 6.5.3 Sensitivity Analysis of the Penman-Monteith Equation

Consider, once again, the comparisons between measured and calculated values of transpiration in the five species studied (Fig. 6.8). In all cases, the Penman-Monteith equation overestimates the transpiration rate after taking into consideration daily variations in environmental variables and stomatal resistance induced by wind speed either directly or indirectly. In an effort to identify possible major contributing factors to these discrepancies a sensitivity analysis of the Penman-Monteith equation was employed. Parameters were set to their average values for each experiment. Average characteristic dimensions were obtained graphically using all possible orientations of the leaves of each species. After computing transpiration

rates at wind speeds from 0.25-5.0 m s<sup>-1</sup> using the above averages, each parameter was varied  $\pm 10\%$  and the resulting percentage change in transpiration rates relative to the 'standard run' at various wind speeds was calculated (Fig. 6.12).

This analysis showed that errors in estimating characteristic dimension by  $\pm 10\%$  resulted in insignificant variation in calculated transpiration rate ( $<2\%$  for these species). Stomatal resistance and ambient temperature each affected the value of terms appearing in both the denominator and numerator of the equation and so have a slightly different effect on variation of transpiration rate if overestimated rather than underestimated. Errors of  $\pm 2^{\circ}\text{C}$  in ambient temperature have a rather small effect which decreases with increasing wind speed from about 5% to 3% in most cases. Since real errors in temperature measurement in these experiments were  $\pm 0.5^{\circ}\text{C}$ , then these errors, as those of characteristic dimension, are unlikely to have been serious. Much more difficult to measure accurately in the wind tunnel were net radiation and saturation vapour pressure deficit, making consideration of these more critical. In the error analysis four out of five cases showed a variation in transpiration rates which decreased with increasing wind speed from about 7% to 3.5% as a result of a postulated  $\pm 10\%$  error in estimating available energy. Although this may seem slight, it is

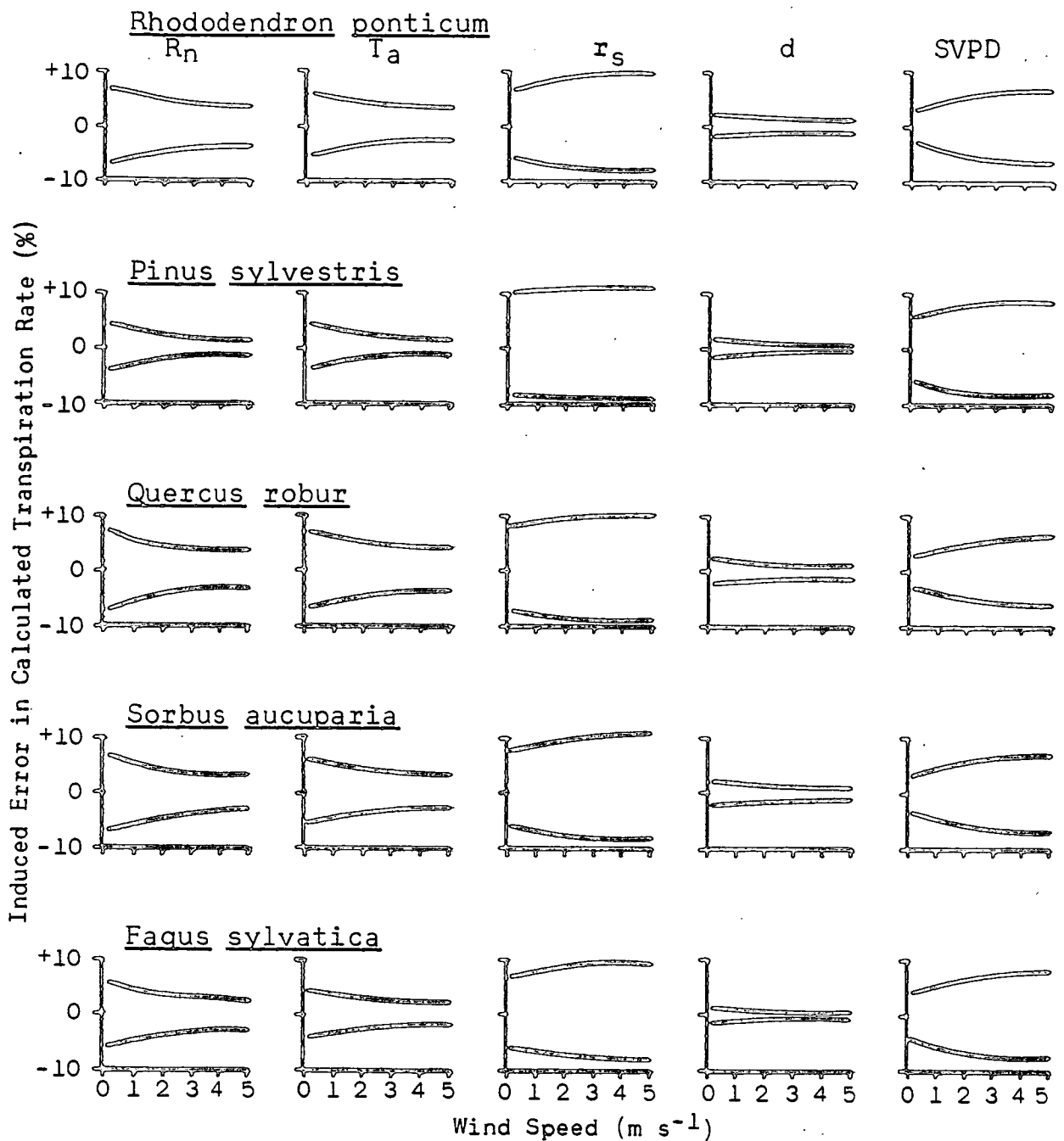


Fig.6.12 Sensitivity analysis of the Penman-Monteith equation in which average values of net radiation ( $R_n$ ), stomatal resistance ( $r_s$ ), characteristic dimension ( $d$ ), and saturation vapour pressure deficit (SVPD) are each varied  $\pm 10\%$ , in turn, and ambient temperature ( $T_a$ ) is varied  $\pm 2^\circ\text{C}$ . The resulting % variation in calculated transpiration (see text) is plotted as a function of wind speed.

likely that net radiation errors exceeded  $\pm 10\%$  resulting in a proportionally greater variation in calculated transpiration.

#### 6.5.4 Reconsideration of Errors in Net Radiation

Net radiation, as measured with the miniature net radiometer, was probably not a good estimate of the radiation absorbed by the leaves in these experiments. There were several reasons for this. Firstly, even though the radiometer was of the miniature kind it nevertheless caused a local disturbance in the radiation regime, mainly by shading. This caused the radiometer to sense a higher net flux than actually prevailed. Secondly, leaves were not horizontal nor uniformly distributed. A leaf with vertical posture, its surfaces facing to leeward and windward, would have absorbed little energy as the radiant flux was mainly from above. Overall, 'average' leaves would have fallen somewhere between the two extremes of being vertical or horizontal.

The net radiometer 'saw' a projected area of foliage and the vantage point of the instrument afforded it a view parallel to that of the major fluxes of incoming radiation. In all the species studied, this projected area was less than the transpiring surface area by some unknown amount. Indeed, the difference between the two areas could conceivably have varied

over a wide range depending on such factors as plant height, vertical distribution of leaf area and leaf sizes and transient differences caused by variations in wind speed. In the context of these experiments, comparisons between observed and calculated transpiration rates were based on measurements of key variables such as  $R_n$ . The measurements and assumptions involved in arriving at values for other variables, such as  $r_a$  and  $r_s$ , were based on the transpiring surface area. Since the sometimes dynamic relationship between transpiring area and projected canopy area was unknown then it was impossible to consider  $R_n$  on the same basis, resulting in an unknown error.

An attempt was made to improve knowledge of the radiation fluxes to leaves in the wind tunnel: this is reported in Appendix D. However, it was not practical to make corrections retrospectively as the canopy structure in the experiments could not be duplicated. Instead, ranges of predicted transpiration rates were calculated, in the case of each species, based on possible  $R_n$  values as suggested by the aforementioned study (Appendix D). These appear in Fig. 6.8 (overlay) and this range of predicted values of transpiration rates tended to agree well with the observed values. Hence, the estimates of  $R_n$  arrived at through a consideration of radiation geometry seemed to provide a basis for realistic predictions of transpiration using the Penman-

Monteith equation, at least in controlled environments.

#### 6.5.5 Errors in Other Parameters

The role of  $R_n$  in determining transpiration, in the case of P. sylvestris, is overshadowed by the relatively large stomatal resistance. When  $r_a$  is so small, as it is in most conifers, even large increases in  $R_n$  do not increase the leaf-air temperature much, and so have little effect on the driving force for transpiration. In fact, Whitehead and Jarvis (1981) propose a simplification of the Penman-Monteith equation, valid for conifers, in which radiation is omitted altogether.

The effect of a  $\pm 10\%$  error in  $r_s$  on variation in calculated transpiration rates increased with increasing wind speed from  $\pm 6\%$  to  $\pm 10\%$  in four cases and in P. sylvestris was between  $\pm 10\%$  and  $\pm 11\%$  at all wind speeds. Values of  $r_s$  were calculated by subtracting  $r_a$  values, obtained using the cooling curve technique on artificial leaves of each species, from values of total resistance obtained from a knowledge of water loss, total transpiring area and leaf-air vapour pressure difference. Therefore, errors in  $r_s$  would be the result of errors in estimating vapour pressure,  $r_a$ , leaf temperature, and gravimetric measurements of water loss.

Errors in estimating saturation deficit of the



atmosphere have greatest effect at high wind but ambient vapour pressure in the wind tunnel was particularly well controlled under these conditions. The relatively minor variations of  $\pm 5\%$  in calculated transpiration rates at the lowest wind speed was not critical.

Errors in the value of  $r_a$ , as determined by the cooling curve technique, would result mainly from radiative coupling of the brass leaf with the surroundings. Grace, et al. (1980) have estimated this systematic error at about  $-7\%$ . Random weighing errors were  $\pm 3\%$  and errors in leaf-air vapour pressure difference, resulting from errors in ambient vapour pressure and leaf temperature, have been estimated as  $\pm 7\%$ , decreasing with increasing wind speed as ambient humidity and temperature control improved.

Since P. sylvestris transpiration rates exhibited such good agreement with calculated rates and since  $r_s$  was the key variable in this case then it was assumed that substantial errors in the estimation of  $r_s$  were unlikely to have occurred. This implicated  $R_n$  in the remaining four species, as having been mainly responsible for the observed discrepancies.

It has been argued here that, in all probability, the values of  $R_n$  used in the Penman-Monteith predictions of transpiration were overestimates. This was probably

due to the difficulty met in obtaining reliable estimates of energy absorbed by individual leaves. Since all other environmental and physiological variables were examined on an individual leaf basis, then the resulting detailed picture of transpiration in these experiments would have been sensitive to the originally crude estimates of  $R_n$ :

#### 6.5.6 Aerodynamic Resistance

Another, though probably less important, consideration is the possible uncertainty in  $r_a$ . In view of the obvious aerodynamic complexity of the potted tree seedlings, both as regards their architecture and their differing types of leaf and leaf posture, it might seem surprising that the results of determining  $r_a$  values for the five species studied agreed so well with laminar boundary layer theory. It is, on the other hand, reasonably well established that leaf posture has very little effect on exchange rates in forced convection (Thom, 1968; Parkhurst, et al. 1968). Moreover, numerous attempts to demonstrate an effect of leaf flutter have failed to do so (Raschke, 1956; Parkhurst, et al. 1968; Parlange, et al. 1971; Grace, 1978). Nevertheless, one would expect substantial shelter effects in a crowded canopy, as shown by Landsberg and Thom (1971) in conifers. Perhaps the agreement with theory, in the

present case, is fortuitous - the tendency of turbulence to increase exchange rates being offset by the shelter effect of nearby leaves. Certainly, unknown errors resulted from the aerodynamic dissimilarity between the real and model leaves. However, it was felt that the faithfulness of the brass replicas coupled with their placement in the aerodynamically complex plant canopy would minimise such errors.

#### 6.5.7 Water Relations

P. sylvestris, the only species which allowed successful measurement of the components of water potential, displayed typical diurnal patterns of total water potential. Concurrent changes in osmotic potential which tended to maintain turgor potential at a steady value suggested a degree of osmoregulation of turgor. However, the plants were never under conditions of water stress which would have tested this hypothesis strenuously. Nevertheless, the relationship between turgor potential and total water potential shown by the plants in this study (Fig. 6.13) did indicate maintenance of turgor within quite small limits.

There are numerous factors affecting osmotic adjustment and obvious benefits to be gained by the plant. The rate of development of stress and degree of stress attained often dictate the limits of the

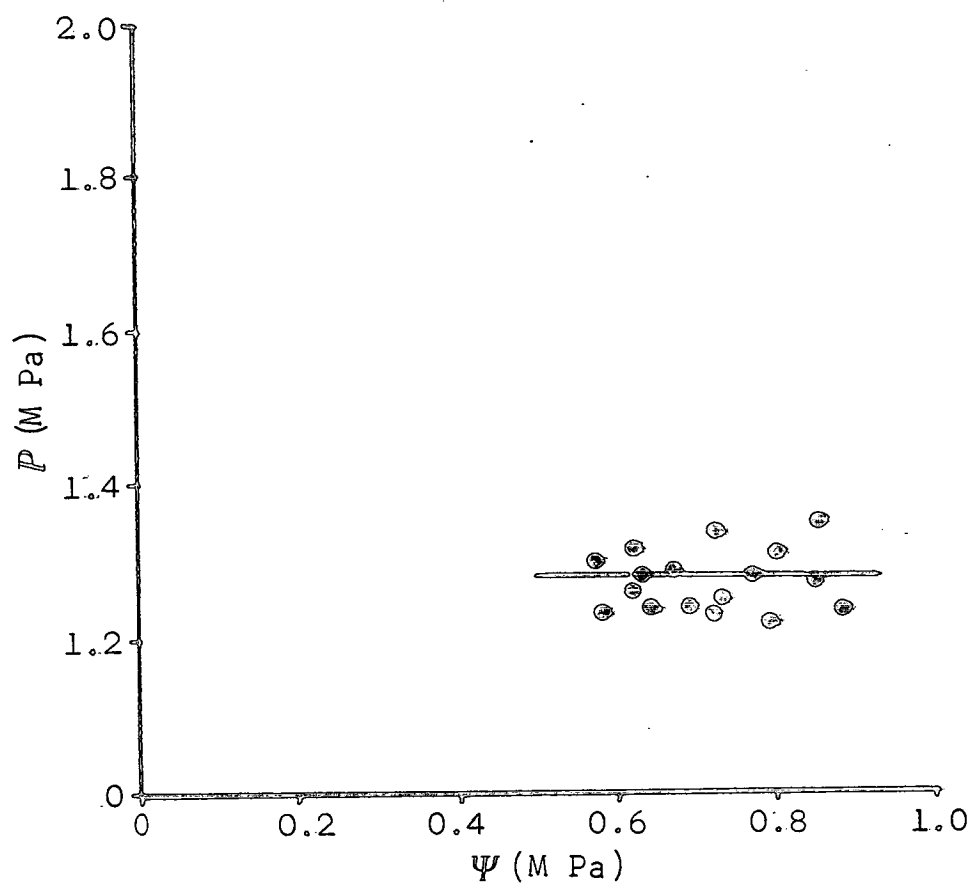


Fig.6.13 Relationship between turgor potential ( $P$ ) and several values of total water potential ( $\Psi$ ) in *Pinus sylvestris*.

role of osmotic adjustment. Jones and Turner (1978) showed that turgor potentials in slowly dried sorghum plants were maintained at higher values than in quickly dried plants at similar total water potentials. Certainly, environmental factors affect drying rates but recent evidence suggests that temperature and light appear to exert direct influence on the degree of osmotic adjustment. Johnson (1978) showed that leaf turgor potential at a particular leaf water potential was higher in six range grasses when grown at 10/5 °C day/night temperature than when grown at 15/10 °C in controlled environment chambers or at 15/15 °C in a glasshouse.

With respect to the effect of light, Turner and Long (1978) found that the osmotic adjustment was only three bars when the quantum flux density at the leaf level was  $650 \mu\text{E m}^{-2}\text{s}^{-1}$ , but was six bars at a higher light level of  $1300 \mu\text{E m}^{-2}\text{s}^{-1}$ .

Some of the benefits of osmotic adjustment which have been demonstrated by researchers in the past include maintenance of cell elongation (Meyer and Boyer, 1972; Hsiao, et al. 1976), maintenance of stomatal opening (Beadle, et al. 1978; Turner, et al. 1978b), maintenance of photosynthesis (Jones and Rawson, 1979), survival of dehydration (Munns, et al. 1979) and exploration of greater soil volume for water (Hsiao, et al. 1976).

Thus, osmotic adjustment of turgor potential has been investigated in many species and a great deal of evidence supports the existence of such a phenomenon (Hsiao and Acevedo, 1974; Hsiao, et al. 1976; Turner, et al. 1978 (a); 1978 (b); Ackerson, et al. 1980). The mechanism by which various species achieve osmotic adjustment has also received attention in the literature. Hastings and Gutknecht (1974), in a study of the giant-celled marine alga, Valonia macrophysa, suggested that a negative feedback loop regulated the turgor pressure. Their results indicated that modification of a component of the plasmalemma cell wall complex (i.e. the pressure transducing mechanism) induced by the hydrostatic pressure gradient led to a reduction of  $K^+$  transport. Zimmermann (1978), in his review, also cited  $K^+$  transport as being important in osmotic adjustment, especially when turgor was increased. Munns, et al. (1979) studied solute accumulation in the apices and leaves of wheat during water stress and found that the main contribution to the initial decline in osmotic potential was from an increase in the content of ethanol-soluble carbohydrates. Subsequent declines during continued water stress were attributed to increases in the concentrations of both carbohydrates and amino acids such as proline and asparagine.

Turner and Jones (1980) presented a discursive review on the subject of turgor maintenance by osmotic

adjustment. They listed soluble sugars, potassium, organic acids, chloride and free amino acids as the range of compounds principally involved and concluded that

"the lowering of the solute potential seems to arise from alteration of existing pathways and translocation patterns in the plant."

P. sylvestris showed a decrease in  $\Psi$  with increasing wind speed. This contradicts the results of Rees (1979) who concluded that wind had little or no effect on  $\Psi$ . However, he used a different species (Pinus contorta) and made only one daily measurement of  $\Psi$  in longer term experiments which considered the effects of two different wind speeds. This may have masked important differences and short term reactions to moderate increases in wind speed. Furthermore, his high wind speed ( $8.5 \text{ m s}^{-1}$ ) was considerably higher than that of these experiments which may have induced stronger physiological control of water loss as suggested by Mellor, et al. (1964).

Finally, the daily decrease in  $\Psi$  was concurrent with an initial increase in transpiration followed by a slight decline in response to increasing wind speed. These data tend to suggest that, within the relatively moderate extremes of wind speed experienced by these plants, transpiration rate changes were mediated by

physical parameters (i.e. VPD and leaf temperature) and some physiological control. However, the degree of physiological response to wind speed was apparently not critical and the plants reacted to the environmental change with an osmotic adjustment which maintained turgor potential. Unfortunately, technical limitations prevented further investigation of these phenomena in the other species tested which would have been obviously illuminating since their responses to increasing wind speed were somewhat different.



## CHAPTER 7. Conclusions

A quantitative understanding of the effects of wind on transpiration requires a knowledge of the plant variables  $r_s$  and  $r_a$ . The environmental variables of concern are the available energy ( $R_n$ ) and the saturation vapour pressure deficit (SVPD) of the surrounding air.

In order to obtain reliable estimates of some of the parameters required to test the Penman-Monteith equation, as well as measurements of certain other important physiological attributes, it was necessary, in some cases, to pay close attention to the application of some existing techniques.

Several technical refinements were achieved in the course of this work. A cheap and reliable thermocouple psychrometer chamber was designed and constructed. Materials were chosen on the basis of an investigation into water uptake rates. It was concluded that chromium plated brass and fluorocarbon rubber (e.g. Viton) were the best to use. Refinements to thermocouple welding techniques allowed routine production of excellent quality psychrometer thermocouple junctions.

In the field of leaf temperature measurements, a cheap thermocouple output amplifier was designed and constructed. This instrument was capable of resolving  $0.01^\circ\text{C}$  temperature differences and was invaluable in assessing cooling curves of brass leaves for estimating

aerodynamic resistance.

The aerodynamic resistance ( $r_a$ ) can be estimated from cooling curves of model leaves. The values so obtained when brass model leaves replaced real leaves in the canopy agreed very well with those calculated from laminar boundary layer theory. Isolated model leaves allowed a degree of scrutiny of the boundary layer which helped to explain the slight discrepancies between observed and calculated exchange rates in these cases. It was shown that for all models except the smooth leaf in laminar flow, there was certainly much turbulence in the boundary layer. Leaf serrations and marginal ripples increased exchange rates somewhat. Coupling power spectrum analysis of turbulence in the boundary layer with the cooling curve technique for measuring heat exchange showed that the enhancement of heat transfer from models with serrations and ripples was apparently related to low turbulence frequencies, especially 200-500Hz.

The stomatal resistance did not change with wind speed as much as has been suggested by other workers. There were, however, some effects:  $r_s$  declined with increasing wind speed in all species except P. sylvestris where there was an increase. Night-time values of transpiration did change somewhat with increasing wind speed, especially in soft-leaved species where they increased irreversibly in the short term. This increase

suggested possible indistinguishable degrees of cuticular and stomatal damage.

Tissue water status could be investigated only in P. sylvestris. It was found that total water potential and osmotic potential decreased with increasing wind speed. Turgor potential was thus maintained at a relatively constant level, suggesting a degree of osmotic adjustment.

Overall, an increase in wind speed usually caused a decline in observed transpiration rates. This was, in particular, due to the drop in leaf-air temperature difference, resulting in a decreased driving force for transpiration. The Penman-Monteith equation predicts the same response under the experimental conditions described.

A sensitivity analysis of the Penman-Monteith equation showed that the measured value of net radiation was particularly crucial to obtaining reliable calculations of transpiration. The geometry of radiation sources and sinks in isolated trees, especially in controlled environments, is, however, complex. Consequently, the energy absorbed by the leaves could not be known with great precision. This limited the comparability of observed data and the Penman-Monteith equation predictions in the present case. However, retrospective consideration does allow a quantitative reassessment of the data which tends to suggest that

the Penman-Monteith equation is a good predictive tool, even when applied to single leaves. However, when the plant is subjected to a fluctuating environment, due consideration must be given to the changes in the physical resistance ( $r_s$ ).

## BIBLIOGRAPHY

- ACKERSON, R.C., KRIEG, D.R., and SUNG, F.J.M. (1980).  
Leaf conductance and osmoregulation of field-grown sorghum genotypes. *Crop Science*, 1, No. 1, 10-14.
- ACOCK, B. (1975). An equilibrium model of leaf water potentials which separates intra- and extra-cellular potentials. *Australian Journal of Plant Physiology*, 2, 253-263.
- BAILEY, I.W., and SINNOTT, E.W. (1916). The climatic distribution of certain types of angiosperm leaves. *American Journal of Botany*, 3, No. 1, 24-39.
- BAKER, K.F. (Ed.) (1957). "System for Producing Healthy Container-Grown Plants, Manual 23." University of California, Division of Agricultural Science.
- BARRS, H.D. (1968). Determination of water deficits in plant tissue. In "Water Deficits and Plant Growth, Volume I." (T.T. Kozlowski, ed.), Academic Press, New York, 390p.
- BEADLE, C.L., TURNER, N.C., and JARVIS, P.G. (1978).  
Critical water potential for stomatal closure in Sitka spruce. *Physiologia Plantarum*, 43, 160-165.
- BEARDSSELL, M.F., JARVIS, P.G., and DAVIDSON, B. (1972).  
A null balance porometer suitable for use with leaves of many shapes. *Journal of Applied Ecology*, 9, 677-690.

- BOYER, J.S. (1969). Measurement of the water status of plants. Annual Review of Plant Physiology, 20, 351-364.
- BROWN, R.W. (1970). Measurement of water potential with thermocouple psychrometers: construction and application. U.S.D.A. Forest Service Research Paper, INT - 80.
- CALDWELL, M.M. (1970). Plant gas exchange at high wind speeds. Plant Physiology, 46, 535-537.
- CAMPBELL, G.S. (1977). "An Introduction to Environmental Physics." Springer-Verlag, New York, 159p.
- CAMPBELL, G.S., TRULL, J.W., and GARDNER, W.H. (1968). A welding technique for Peltier thermocouple psychrometers. Soil Science Society American Proceedings, 32, 887-889.
- CHAMBERLAIN, A.C. (1968). Transport of gases to and from surfaces with bluff and wave-like roughness elements. Quarterly Journal of the Royal Meteorological Society, 94, No. 401, 318-332.
- CLARK, J.A. (1975). Energy transfer and surface temperature over plants and animals. In "Light as an Ecological Factor. II." 16th Symposium of the British Ecological Society, (G.C. Evans, R. Bainbridge, and O. Rackham, eds.), Blackwell Scientific Publications, London, 616p.
- DAUBENMIRE, R.F. (1959). "Plants and Environment." John Wiley and Sons, Incorporated, New York, 422p.

- DIXON, M.A., THOMPSON, R.G., and FENSOM, D.S. (1978).  
Electrical resistance measurements of water  
potential in avocado and white spruce. Canadian  
Journal of Forest Research, 8, No. 1, 73-80.
- DRAKE, B.G., RASCHKE, K., and SALISBURY, F.B. (1970).  
Temperature and transpiration resistances of  
Xanthium leaves as affected by air temperature,  
humidity and wind speed. Plant Physiology, 46,  
324-330.
- EDWARDS, W.R.N. (1981). Flow of water in trees. Ph.D.  
Thesis, Department of Forestry and Natural Resources,  
University of Edinburgh, Edinburgh, Scotland.
- van EIMERN, J., KARSCHON, R., RAZUMOVA, L.A., and  
ROBERTSON, G.W. (1964). "Windbreaks and Shelter-  
belts", Technical Note 59, World Meteorological  
Organisation, No. 147, 70TP, Geneva, Switzerland,  
188p.
- FENSOM, D.S. (1966). On measuring electrical resistance  
in situ in higher plants. Canadian Journal of  
Plant Science, 46, 169-175.
- FRANK, A.B., and WILLIS, W.D. (1972). Influence of  
windbreaks on leaf water status in spring wheat.  
Crop Science, 12, 668-672.
- GAASTRA, P. (1959). Photosynthesis of crop plants as  
influenced by light, carbon dioxide, temperature  
and stomatal diffusion resistance. Mededelingen  
van de Landbouwhogeschool te Wageningen, 59, No.  
13, 1-68.

- GATES, D.M., and PAPIAN, L.E. (1971). "Atlas of Energy Budgets of Plant Leaves." Academic Press, New York, 277p.
- GRACE, J. (1974). The effect of wind on grasses. I. Cuticular and stomatal transpiration. Journal of Experimental Botany, 25, 542-551.
- GRACE, J. (1977). "Plant Response to Wind." Academic Press, London, 204p.
- GRACE, J. (1978). The turbulent boundary layer over a flapping Populus leaf. Plant, Cell and Environment, 1, 35-38.
- GRACE, J. (1981). Some effects of wind on plants. In "Plants and Their Atmospheric Environment." 21st Symposium of the British Ecological Society, (J. Grace, E.D. Ford, and P.G. Jarvis, eds.), Blackwell Scientific Publications, Oxford, 419p.
- GRACE, J., FASEHUN, F.E., and DIXON, M.A. (1980). Boundary layer conductances of the leaves of some tropical timber trees. Plant, Cell and Environment, 3, 443-450.
- GRACE, J., and WILSON, J. (1976). The boundary layer over a Populus leaf. Journal of Experimental Botany, 27, 231-241.
- HANRATTY, T.J. (1969). The use of electrochemical techniques to study flow fields and mass transfer rates. International Seminar on Heat and Mass Transfer in Flows with Separated Regions and Measurement Techniques, Herceg-Novi, 1-13 September.



- HASTINGS, D.F., and GUTKNECHT, J. (1974). Turgor pressure regulation: modulation of active potassium transport by hydrostatic pressure gradients. In "Membrane Transport in Plants." (U. Zimmermann and J. Dainty, eds.), Springer-Verlag, Berlin, 79-83.
- HAYDEN, R.E., DIONNE, L., and FENSOM, D.S. (1972). Electrical impedance studies of stem tissue of Solanum clones during cooling. Canadian Journal of Botany, 50, 1547-1554.
- HAYDEN, R.I., MOYSE, D., CALDER, F.W., CRAWFORD, D.P., and FENSOM, D.S. (1969). Electrical impedance studies on potato and alfalfa tissue. Journal of Experimental Botany, 20, No. 63, 177-200.
- HELLKVIST, J., RICHARDS, G.P., and JARVIS, P.G. (1974). Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber. Journal of Applied Ecology, 11, 637-667.
- HSIAO, T.C., and ACEVEDO, E. (1974). Plant responses to water deficits, water-use and efficiency, and drought resistance. Agricultural Meteorology, 14, 59-84.
- HSIAO, T.C., ACEVEDO, E., FERERES, E., and HENDERSON, D.W. (1976). Stress metabolism. Philosophical Transactions of the Royal Society of London, B, 273, 479-500.

- IDLE, D.B. (1968). The measurement of apparent surface temperature. In "The Measurement of Environmental Factors in Terrestrial Ecology." 8th Symposium of the British Ecological Society, (R.N. Wadsworth, ed.), Blackwell Scientific Publications, Oxford, 314p.
- JARVIS, P.G. (1971). The estimation of resistances to carbon dioxide transfer. In "Plant Photosynthetic Production, Manual of Methods." (Z. Sestak, J. Catsky, and P.G. Jarvis, eds.), Junk, The Hague, 818p.
- JARVIS, P.G. (1981). Stomatal conductance, gaseous exchange and transpiration. In "Plants and Their Atmospheric Environment." 21st Symposium of the British Ecological Society, (J. Grace, E.D. Ford, and P.G. Jarvis, eds.), Blackwell Scientific Publications, Oxford, 419p.
- JOHNSON, D.A. (1978). Environmental effects on turgor pressure response in range grasses. Crop Science, 18, 945-948.
- JONES, M.M., and RAWSEN, H.M. (1979). Influence of rate of development of leaf water deficits upon photosynthesis, leaf conductance, water use efficiency, and osmotic potential in sorghum. *physiologia Plantarum*, 45, 103-111.
- JONES, M.M., and TURNER, N.C. (1978). Osmotic adjustment in leaves of sorghum in response to water deficits. *Plant Physiology*, 61, 122-126.
- KANEMASU, E.T., THURTELL, G.W., and TANNER, C.B. (1969). Design, calibration and field use of a stomatal diffusion porometer. *Plant Physiology*, 44, 881-885.

- KUMAR, A., and BARTHAKUR, N. (1971). Convective heat transfer measurements of plants in a wind tunnel. *Boundary Layer Meteorology*, 2, 218-227.
- LANDSBERG, J.J., and THOM, A.S. (1971). Aerodynamic properties of a plant of complex structure. *Quarterly Journal of the Royal Meteorological Society*, 97, 565-570.
- LEWIS, J.S. (1971) A heat/mass transfer analogy applied to fully developed turbulent flow in an annulus. *Journal of Mechanical Engineering Science*, 13, 268-292.
- LINACRE, E.T. (1964). Determinations of heat transfer coefficient of a leaf. *Plant Physiology*, 39, 687-690.
- LINACRE, E.T. (1967). Further studies of the heat transfer from a leaf. *Plant Physiology*, 5, No. 5, 651-658.
- LOPUSHINSKY, W., and KLOCK, G. (1970). Construction details of ceramic bulb psychrometers. Mimeo. U.S.D.A. Forest Service, Forest Hydrology Laboratory, Wenatchee, Washington.
- MacKERRON, D.K.L. (1976). Wind damage to the surface of strawberry leaves. *Annals of Botany*, 40, 351-354.
- MARSHALL, J.K. (1967). The effect of shelter on the productivity of grasslands and field crops. *Field Crop Abstracts*, 20, 1-14.
- MARTIN, E.V., and CLEMENTS, F.E. (1935). Studies of the effect of artificial wind on growth and transpiration in Helianthus annuus. *Plant Physiology*, 10, 613-636.

- MELLOR, R.S., SALISBURY, F.B., and RASCHKE, K. (1964).  
Leaf temperatures in controlled environments.  
Planta, 61, 56-72.
- MERRILL, S.D., DALTON, F.N., HERKELRATH, W.N., HOFFMAN,  
G.J., INGVALSON, R.D., OSTER, J.D., and RAWLINS,  
S.L. (1968). Details of construction of a multi-  
purpose thermocouple psychrometer. Research Report  
No. 155, United States Salinity Laboratory, A.R.S.-  
U.S.D.A., Riverside, California.
- METEOROLOGICAL OFFICE (1964). Hygrometric Tables, Part  
3, Second Edition. Aspirated Psychrometer Readings,  
Degrees Celsius, Her Majesty's Stationary Office,  
London.
- MEYER, R.F., and BOYER, J.S. (1972). Sensitivity of  
cell division and cell elongation to low water  
potentials in soybean hypocotyls. Planta, 108, 77-87.
- MILLAR, B.D. (1971a). Improved thermocouple psychrometer  
for the measurement of plant and soil water  
potential. I. Thermocouple psychrometry and an  
improved instrument design. Journal of Experimental  
Botany, 22, 875-890.
- MILLAR, B.D. (1971b) Idem. II. Operation and calibration.  
Journal of Experimental Botany, 22, 891-905.
- MILLAR, B.D. (1971c). Idem. III. Equilibration. Journal  
of Experimental Botany, 25, 1070-1084.
- MONTEITH, J.L. (1965) Evaporation and environment. In  
"The State and Movement of Water in Living Organisms."  
Symposium of the Society for Experimental Biology,  
Cambridge University Press, 19, 205-234.

- MONTEITH, J.L. (1973). "Principles of Environmental Physics." Arnold, London, 241p.
- MONTEITH, J.L. (1981). Coupling of plants to the atmosphere. In "Plants and Their Atmospheric Environment." 21st Symposium of the British Ecological Society, (J. Grace, E.D. Ford, and P.G. Jarvis, eds.), Blackwell Scientific Publications, Oxford, 419p.
- MUNNS, R., BRADY, C.J., and BARLOW, E.W.R. (1979). Solute accumulation in the apex and leaves of wheat during water stress. Australian Journal of Plant Physiology, 6, 379-389.
- MURPHY, C.E., and KNOERR, K.R., (1977). Simultaneous determinations of the sensible and latent heat transfer coefficients for tree leaves. Boundary Layer Meteorology, 11, 223-241.
- NEAL, S.B.H.C. (1975). The development of the thin-film naphthalene mass-transfer analogue technique for the direct measurement of heat-transfer coefficients. International Journal of Heat and Mass Transfer, 18, 559-567.
- NEAL, S.B.H.C., NORTHOVER, E.W., and HITCHCOCK, J.A. (1970). The development of a technique for applying naphthalene to surfaces for mass transfer analogue investigations. Journal of Physics E; Scientific Instruments, 3, 636-638.

- PARKHURST, D.F., DUNCAN, P.R., GATES, D.M., and KREITH, F. (1968). Wind tunnel modelling of convection of heat between air and broad leaves of plants. *Agricultural Meteorology*, 5, 33-47.
- PARKINSON, K.J., and DAY, W. (1980). Temperature corrections to measurements made with continuous flow porometers. *Journal of Applied Ecology*, 17, 457-460.
- PARLANGE, J.Y., WAGGONER, P.E., and HEICHEL, G.H. (1971). Boundary layer resistance and temperature distribution on still and flapping leaves. *Plant Physiology*, 48, 437-442.
- PEARMAN, G.I., WEAVER, H.L., and TANNER, C.B. (1972). Boundary layer heat transfer coefficients under field conditions. *Agricultural Meteorology*, 10, 83-92.
- PECK, A.J. (1968). Theory of the Spanner psychrometer. I. The thermocouple. *Agricultural Meteorology*, 5, 433-447.
- PECK, A.J. (1969). Idem. II. Sample effects and equilibration. *Agricultural Meteorology*, 6, 111-124.
- PENMAN, H.L. (1948). Natural evaporation from open water, bare soil and grass. *Proceedings of the Royal Society, London, A*, 193, 120-145.
- PERRIER, A. (1971). Leaf temperature measurement. In "Plant Photosynthetic Production, Manual of Methods." (Z.Sestak, J. Catsky, and P.G. Jarvis, Eds.), Junk, The Hague, 632-672.

- RASCHKE, K. (1956). Über die physikalischen besiehungen zwischen warmenbergangszahl, strahlungsaustausch, temperature und transpiration eines blattes. *Planta*, 48, 200-238.
- RASCHKE, K. (1960). Heat transfer between the plant and the environment. *Annual Review of Plant Physiology*, 11, 111-126.
- RAWLINS, S.L. (1966). Theory for thermocouple psychrometers used to measure water potential in soil and plant samples. *Agricultural Meteorology*, 3, 293-310.
- REES, D. (1979). The effects of wind and shaking on the morphology, growth, gas exchange and water relations of Pinus contorta (Douglas). Ph.D. Thesis, Department of Forestry and Natural Resources, University of Edinburgh, Edinburgh, Scotland.
- RICHARDS, P.W. (1952). "The Tropical Rain Forest." Cambridge University Press, 450p.
- ROSENBERG, N.J. (1966). Microclimate, air mixing and physiological regulation of transpiration as influenced by wind shelter in an irrigated bean field. *Agricultural Meteorology*, 3, 197-224.
- SATOO, T. (1951a). Leaf temperature in relation to the influence of wind on transpiration of plants. I. *Bulletin of Tokoyo University Forests*, 39, 31-38.
- SATOO, T. (1951b). Idem. II. *Bulletin of Tokoyo University Forests*, 39, 39-43.

- SATOO, T. (1951c). Idem. III. Bulletin of Tokoyo, University Forests, 39, 49-54.
- SATOO, T. (1962). Wind transpiration and tree growth. In "Tree Growth." (T.T. Kozlowski, ed.), Ronald Press Company, New York, 299-310.
- SCHOLANDER, P.F., and HAMMEL, H.T. (1965). Sap pressure in vascular plants. Science, 148, 339-346.
- SCHUBAUER, G.B., and SKRAMSTAD, H.K. (1947). Laminar boundary-layer oscillations and stability of laminar flow. Journal of the Aeronautical Sciences, 14, No. 2, 69-78.
- SCHUEPP, P.H. (1972). Studies of forced convection heat and mass transfer of fluttering realistic leaf models. Boundary Layer Meteorology, 2, 263-274.
- SCHUEPP, P.H. (1973). Model experiments on free convection heat and mass transfer of leaves and plant elements. Boundary Layer Meteorology, 3, 454-467.
- SCUTT, H.R., SHIGO, A.L., and LESSARD, R.A. (1972). Detection of discolored and decayed wood in living trees using a pulsed electric current. Canadian Journal of Forest Research, 2, 54-56.
- SKIDMORE, E.L., and HAGEN, L.J. (1970). Evaporation in sheltered areas as influenced by windbreak porosity. Agricultural Meteorology, 7, 363-374.
- SKIDMORE, E.L., JACOBS, H.S., and HAGEN, L.J. (1972). Microclimate modification by slat-fence windbreaks. Agronomy Journal, 64, 160-162.



- SPANNER, D.C. (1951). The Peltier effect and its use in the measurement of suction pressure. *Journal of Experimental Botany*, 2, 145-168.
- TALBOT, A.J.B., TYREE, M.T., and DAINITY, J. (1975). Some notes concerning the measurement of water potentials of leaf tissue with specific reference to Tsuga canadensis and Picea abies. *Canadian Journal of Botany*, 53, No. 8, 784-788.
- THOFELT, L. (1975). Studies on leaf temperature recorded by direct measurement and by thermography. Ph.D. Thesis, Uppsala University, Sweden.
- THOM, A.S. (1968). The exchange of momentum, mass and heat between an artificial leaf and the airflow in a wind tunnel. *Quarterly Journal of the Royal Meteorological Society*, 94, 44-55.
- THOM, A.S. (1975). Momentum, mass and heat exchange of plant communities. In "Vegetation and the Atmosphere." (J.L. Monteith, ed.), Academic Press, London, 278p.
- THOMPSON, J.R. (1974). The effect of wind on grasses. II. Mechanical damage in Festuca arundinacea Schreb. *Journal of Experimental Botany*, 25, 965-972.
- THOMPSON, J.R. (1975). Effects of wind on the growth and productivity of grasses with special reference to tall fescue (Festuca arundinacea Schreb.). Ph.D. Thesis, University of Edinburgh, Scotland.
- TIBBALS, E.C., CARR, E.K., GATES, D.M., and KREITH, F. (1964). Radiation and convection in conifers. *American Journal of Botany*, 51, 529-538.

- TRANQUILLINI, W. (1969). Photosynthese und transpiration einiger holzarten bei verschieden starken wind. Zentralblatt fur das Gesamte Forstwesen, 81, 35-48.
- TURNER, N.C., BEGG, J.E., RAWSON, H.M., ENGLISH, S.D. and HEARN, A.B. (1978a). Agronomic and physiological responses of soybean and sorghum crops to water deficits. III. Components of leaf water potential, leaf conductance,  $^{14}\text{CO}_2$  photosynthesis and adaptation to water deficits. Australian Journal of Plant Physiology, 5, 179-194.
- TURNER, N.C., BEGG, J.E., and TONNET, M.L. (1978b). Osmotic adjustment of sorghum and sunflower crops in response to water deficits and its influence on the water potential at which stomata close. Australian Journal of Plant Physiology, 5, 597-608.
- TURNER, N.C., and JONES, M.M. (1980). Turgor maintenance by osmotic adjustment: a review and evaluation. In "Adaptation of Plants to Water and High Temperature Stress." (N.C. Turner and P.J. Kramer, eds.), John Wiley and Sons, New York and Toronto, 482p.
- TURNER, N.C., and LONG, M.J. (1978). Influence of rate of drying and quantum flux densities on the water status and osmotic adjustment of sorghum. C.S.I.R.O., Division of Plant Industry Annual Report, 93.
- TURNER, N.C., and PARLANGE, J.Y. (1970). Analysis of operation and calibration of a ventilated diffusion porometer. Plant Physiology, 46, 175-177.

- TYREE, M.T., DAINITY, J., and BENIS, M. (1972). The water relations of hemlock (Tsuga canadensis). I. Some equilibrium water relations as measured by the pressure-bomb technique. Canadian Journal of Botany, 51, 1471-1479.
- TYREE, M.T., and HAMMEL, H.T. (1972). The measurement of the turgor pressure and the water relations of plants by the pressure bomb technique. Journal of Experimental Botany, 23, No. 74. 267-282.
- WESCOR, INCORPORATED (1974). HR-33T Instruction Manual. Logan, Utah.
- WHITEHEAD, D., and JARVIS, P.G. (1981). Coniferous forests and plantations. In "Water Deficits and Plant Growth, Volume VI." Academic Press, London, 49-152.
- WIEBE, H.H., CAMPBELL, G.S., GARDNER, W.H., RAWLINS, S.L., CARY, J.W., and BROWN, R.W. (1971). "Measurement of Plant and Soil Water Status." Bulletin 484, Utah Agricultural Experiment Station, Logan, 71p.
- WIGLEY, G., and CLARK, J.A. (1974). Heat transport coefficients for constant energy flux models of broad leaves. Boundary Layer Meteorology, 7, 139-150.
- WILSON, J. (1978). Some physiological responses of Acer pseudoplatanus L. to wind at different levels of soil water, and the anatomical features of abrasive leaf damage. Ph.D. Thesis, Department of Forestry and Natural Resources, University of Edinburgh, Edinburgh, Scotland.

- WOODS, F.W., HOUGH, W.A., O'NEAL, D.O., and BARNETT, J.  
(1965). Gamma-ray attenuation by Loblolly pine wood:  
an investigation of integral counting. Forest  
Science, 11, 41-45.
- YAMAOKA, Y. (1958). Total transpiration from a forest.  
Transactions of the American Geophysical Union,  
39, 266-272.
- ZIMMERMANN, U. (1978). Physics of turgor and osmo-  
regulation. Annual Review of Plant Physiology, 29,  
121-148.

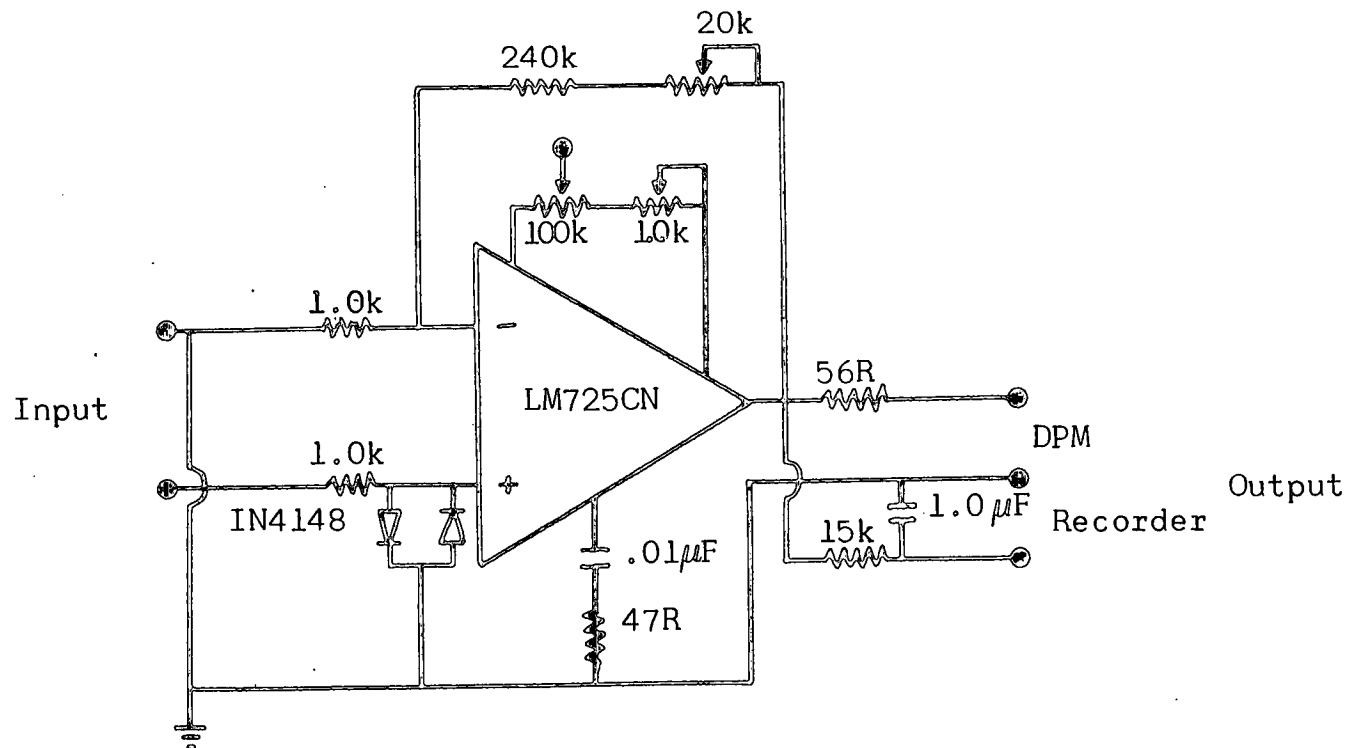


Fig.A.1 Circuit and components for thermocouple output amplifier.

APPENDIX B.

Water Uptake by Some Chamber Materials

by

M. Dixon and J. Grace

This appendix comprises a short paper which has been accepted for publication in Plant, Cell and Environment, and should appear in 1982.

## ABSTRACT

The characteristics of water uptake by several materials have been studied. Nitrile rubber, silicone rubber and perspex retained substantial quantities of water. Metals took up smaller, but still significant, amounts of water, and glass was the least water-retentive material used in the tests. The surface structure of the material, revealed by scanning electron microscopy, did not necessarily account for its water uptake characteristics. The results are discussed in relation to the design and construction of psychrometer and porometer chambers.

## INTRODUCTION

There are several techniques in the plant sciences in which a knowledge of the water uptake properties of the apparatus is crucial. Perhaps the most critical case is the thermocouple psychrometer chamber (Millar, 1971a, b, 1974; Wiebe, Campbell, Gardner, Rawlins, Cary and Brown, 1971). In such a chamber a sample of leaf tissue is allowed to exchange water vapour with a small volume of air until an equilibrium condition is achieved. At this equilibrium the water potential of the leaf material is related to the humidity of the air in the chamber (Spanner, 1951; Rawlins, 1966). Any tendency of the walls of this chamber to take up water will have at least two undesirable consequences. Firstly, the time taken to achieve equilibrium may be unduly prolonged - this is extremely inconvenient when attempting to obtain a diurnal course of water potential with a small number of psychrometer units. Secondly, it is possible that true equilibrium may never be obtained as a result of wall porosity, and thus an absolute error may be introduced.

The other apparatus in which water uptake problems commonly occur include assimilation chambers and porometers (Stigter, Birnie and Lammers, 1973).

Materials used in the construction of these chambers include metals, plastics (especially Perspex, known as Plexiglass in North America), and various rubber



compounds as sealing gaskets. Very little information is available on the rates of water uptake of these materials under realistic conditions. One paper, frequently referred to, reports measurements on such materials, but these results may be spuriously high as condensation occurred on the samples; moreover, no indication was given of the kinetics of uptake (Shepherd, 1973).

The present work was undertaken to enlarge upon Shepherd's findings and enable a rational choice of materials with which to construct a thermocouple psychrometer unit.

#### MATERIALS AND METHODS

Samples of eleven materials (Table 1), each of surface area  $2-4\text{cm}^2$ , were suspended over silica gel in a sealed desiccation jar for six days. The resulting dry weight of each sample was then measured to the nearest microgram using a Cahn Automatic Electrobalance, Model 4700; and the sample suspended over a saturated aqueous solution of sodium sulphate ( $\text{Na}_2\text{SO}_4 \cdot 10\text{H}_2\text{O}$ ) in a sealed jar. The jar was placed in a water bath at  $20^\circ\text{C} \pm 0.01^\circ\text{C}$ ). Such conditions produced a constant humidity of 93% over the solution (Weast, 1971) and eliminated the possibility of condensation on the samples. The weight of each sample was determined at intervals until twenty-four hours had elapsed when the samples were

TABLE 1.. List of materials used in tests, with full specification where appropriate.

<u>MATERIAL</u>	<u>SPECIFICATION</u>
Butadiene-acrylonitrile	Walker's medium nitrile (80 I.R.H.D.)
Fluorocarbon rubber	Walker's 'Viton' (80 I.R.H.D.)
Silicone rubber	Walker's silicone rubber (70 I.R.H.D.)
Polytetrafluoroethylene	Walker's 'Fluolion' PTFE
Acrylic plastic	'Perspex' sheet
Glass	Cover Slip, BS 53836-17
Stainless steel	BS 18/8
Brass, polished	Hard rolled
Brass, tarnished	Hard rolled
Nickel	Electroplated on brass, 15 $\mu$ m thick
Nickel-chrome	Electroplated on brass, 30 $\mu$ m thick

returned to a desiccation jar. The samples were again weighed at intervals until their initial dry weights were restored.

The surface of each sample was photographed under the scanning electron microscope, after sputter-coating the non-conductive materials with gold (Polaron, Model E5000).

## RESULTS AND DISCUSSION

Water uptake rates and absolute levels of water retained are shown in Fig. 1. Some materials take up considerable amounts of water and require many hours to reach an equilibrium, so would not be suitable for the construction of chambers. Plastic and rubber materials are particularly undesirable, though when they must be used, as in sealing rings on psychrometer chambers, it should be noted that some are better than others. Viton, for its low uptake level, and silicone rubber for its rapid rate of water loss may be suitable for this purpose but ordinary O-rings of nitrile rubber are especially poor. Viton is more practical than silicone rubber as an O-ring material, as the latter is too compressible and creates variation in sealing pressure, which in turn affects instrument sensitivity (Wiebe et al. 1971). Polytetrafluoroethylene (PTFE) took up very little water, but O-rings made of it are too hard and do not readily make a seal.

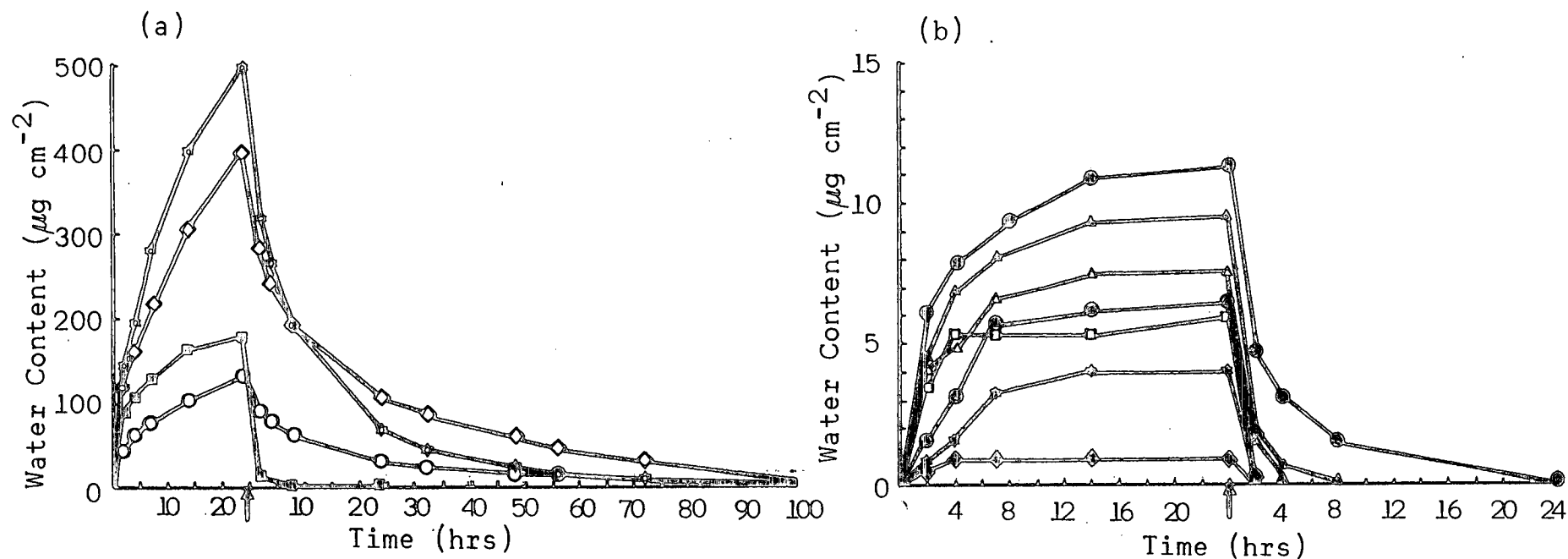


Fig.1 The characteristics of water uptake and loss for the materials listed in Table 1. Symbols represent nitrile rubber ( $\star$ ), Perspex ( $\diamond$ ), silicone rubber ( $\boxtimes$ ), Viton ( $\circ$ ), tarnished brass ( $\odot$ ), stainless steel ( $\Delta$ ), brass ( $\triangle$ ), nickel ( $\odot$ ), Fluorlon PTFE ( $\square$ ), nickel-chrome ( $\star$ ), glass ( $\diamond$ ). The arrow indicates the time when the samples were removed from the hydrated atmosphere. (Note the differences in scale between (a) and (b).)

The relatively low uptake levels and retention periods of the metallic and electroplated samples, as well as the PTFE sample, show them to be quite suitable as chamber wall materials. Especially unsuitable is brass, as the tarnished brass achieved the highest level of water uptake of the metals and the longest retention period. The relationship between polished (Plate 1.B) and tarnished brass (Plate 1.A) can probably be taken as the general case when comparing oxidised and polished surfaces of the same metal. The porous surface of the stainless steel sample (Plate 1.F) may account for its poor performance compared to the electro-plated brass samples (Plates 1.C and 1.D). The diffusion of water vapour into pores cannot itself account for observed gains in weight as water-saturated air is less dense than dry air. Rather, it is necessary to postulate the adsorption of water molecules onto the much increased wall area provided by a porous system.

Within the metals, the rougher surfaces tended to display the highest levels of uptake: within the plastics and rubbers, silicone rubber and Viton have quite rough surfaces (Plate 2) yet relatively low levels of water uptake. It is presumed that water is taken up into intermolecular lacunae which are not visible under SEM (Barrie and Platt, 1963).

The absolute levels of uptake reported here are less than those given by Shepherd (1973), who exposed

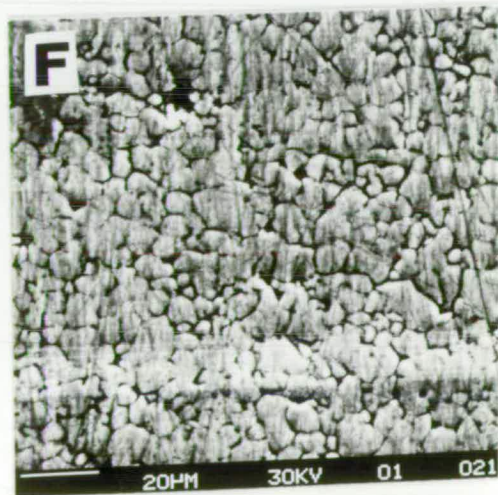
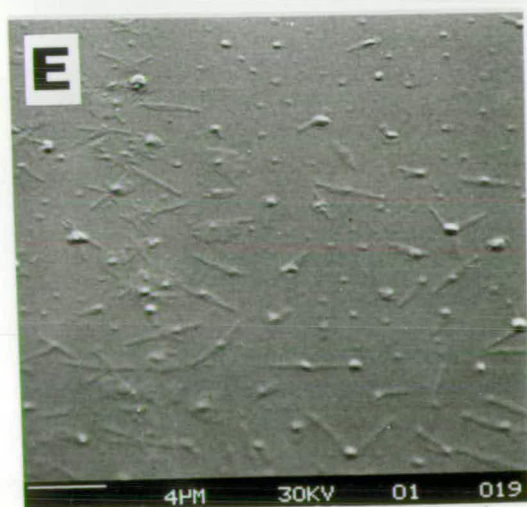
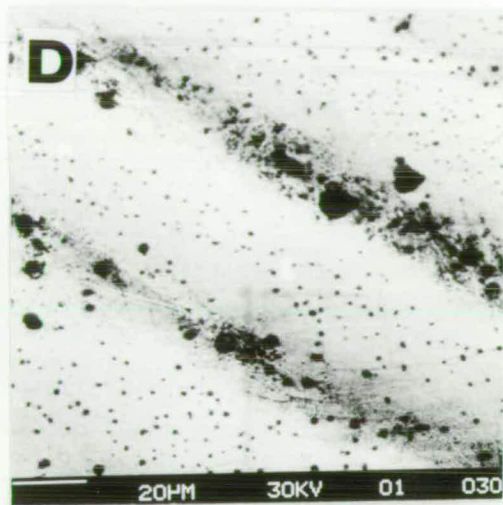
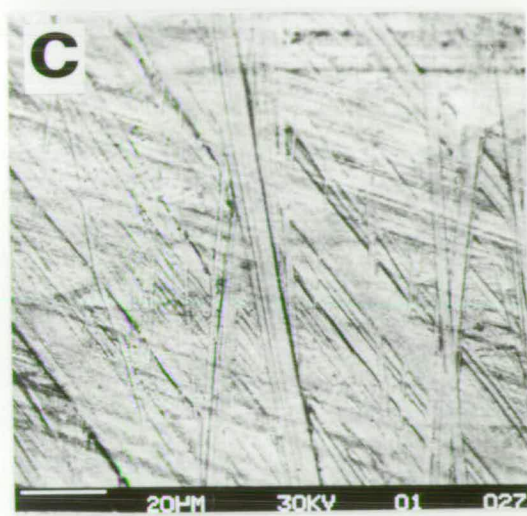
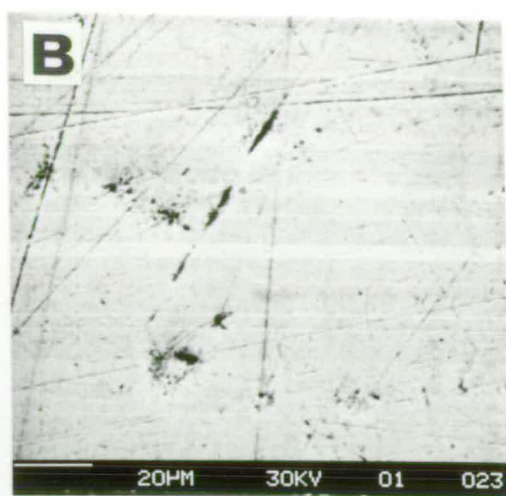
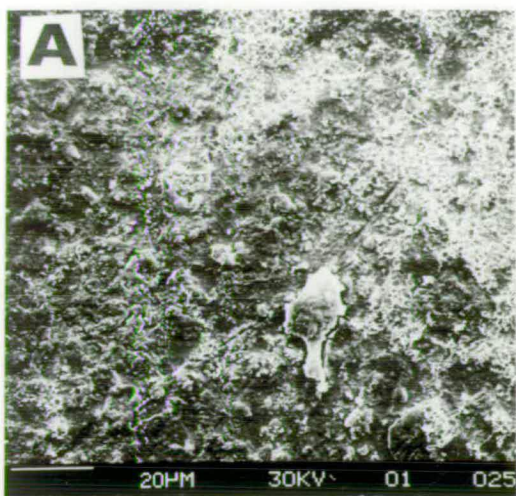
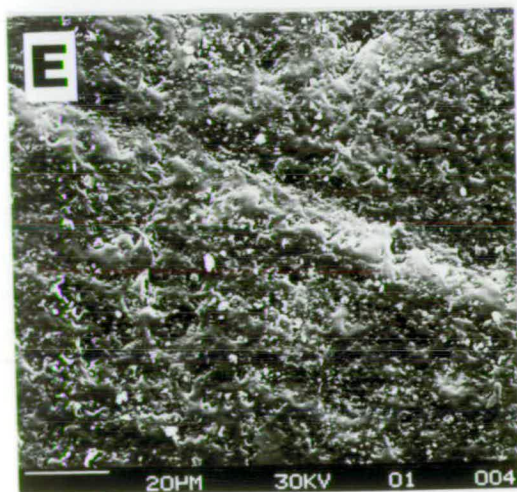
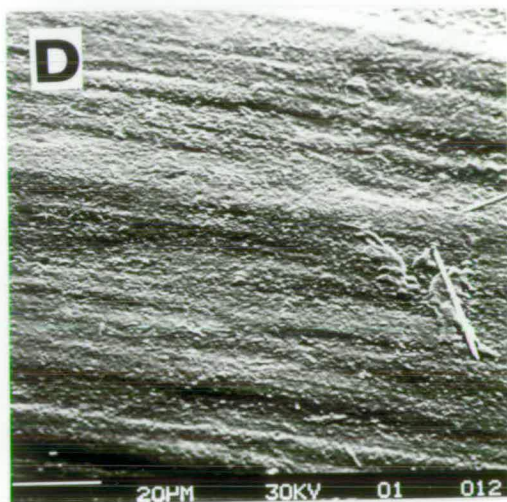
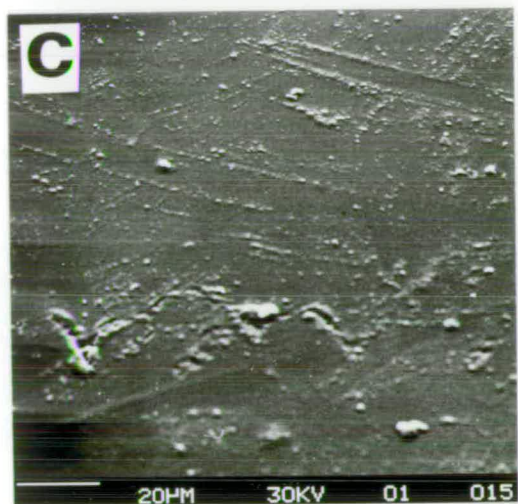
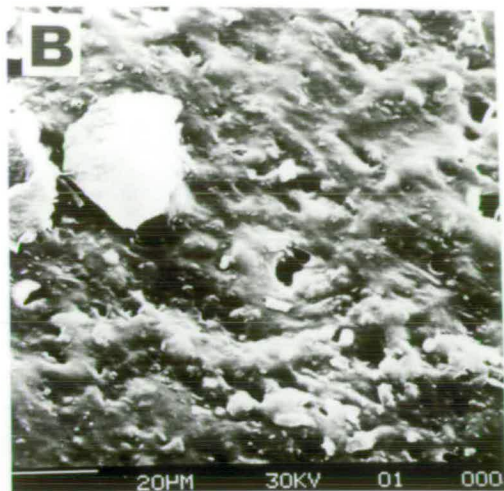
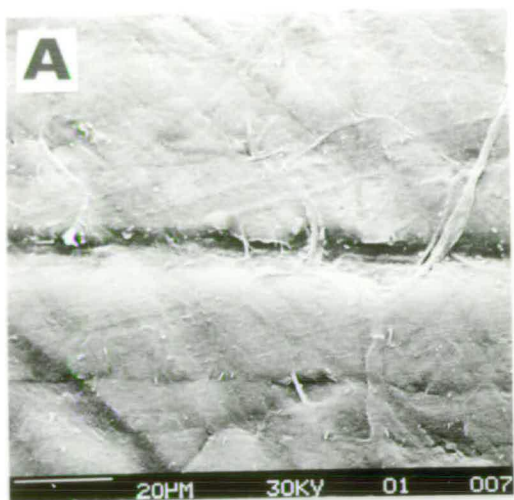


Plate 2 Fine structure of the surfaces of plastics and rubbers: A, Fluolion PTFE; B, silicone rubber; C, Perspex; D, nitrile rubber; E, Viton.







similar sample materials for 24 hours over distilled water. For example, his level of water uptake for PTFE is almost twenty times more than that found in this study. This discrepancy is probably due to the condensation, which he admits occurred in his experiment, requiring that the samples be blotted before weighing. Condensation was prevented in the present study by the use of an incompletely saturated atmosphere.

There is strong evidence to suggest that many difficulties involved in the use of thermocouple psychrometers arise due to water uptake by the walls of the chamber. In particular, the long equilibration time observed by most workers is not only inconvenient, but may introduce absolute errors due to metabolic changes which necessarily occur within the tissue over several hours following excision. Equilibration times exceeding five hours are frequently required, even when using calibration solutions (Barrs and Slatyer, 1965; Lambert and van Schilfgaarde, 1965). Moreover, Lambert and van Schilfgaarde (1965) and Millar (1971a) report different equilibration times in psychrometer chambers made from different materials. Millar found that brass and stainless steel chambers equilibrated more rapidly than those of polythene and teflon, whilst epoxy-resin, rubber and perspex chambers took especially long to equilibrate. The long equilibration time has led some authors to adopt a special chamber geometry, so that

the sensing thermocouple is shielded from the walls: in this way a satisfactory reading can sometimes be obtained before a true equilibrium has occurred (Peck 1969; Millar, 1974).

It is also observed, when calibrating psychrometer chambers, that the calibration line does not pass through the origin; that is, for pure water the unit develops a finite voltage output which may correspond to several bars. Most workers accept this and incorporate it into the calibration, claiming it to be fully reproducible as long as a standard equilibration time is employed (Wiebe et al, 1971). However, we have found rather poor reproducibility with aluminium chambers and think it is the result of water uptake on the walls. The niches and channels in metallic walls behave as tortuous extensions of the chamber volume which in an extreme case could be infinite. In a completely dry chamber, they take a long time to equilibrate with the main chamber volume and in a wet chamber they become an unwanted source of water vapour, so that the final equilibrium humidity is excessively high.

It is useful to compare the mass of water in the walls with that in the chamber volume and in the leaf sample. As an example, a chamber designed to accept leaf discs typically may have a volume of  $0.5\text{cm}^3$  which, at equilibrium, contains air nearly saturated with water vapour - about  $4\mu\text{g}$  of water. Its exposed wall area might

be about  $3\text{cm}^2$  with perhaps a further  $0.2\text{cm}^2$  of exposed rubber sealing ring. Reference to Fig. 1 show that the total surface area surrounding the volume has the capacity to take up far more water vapour than the  $4\mu\text{g}$  present in the chamber air. It follows that the equilibration characteristics of the whole unit will be mainly determined by those of the wall material. The water content of a leaf disc cut to fit on the floor of this chamber might be about  $0.1\text{g}$ , probably adequate to provide enough water to saturate the whole system with water vapour without itself suffering much decline in water potential. The leaf discs themselves may contribute to the variability in equilibration characteristics: the cuticle and epicuticle may take up water vapour despite their hydrophobic properties (Millar, 1974) and the cuticular resistance will be a factor affecting equilibrium (Peck, 1969). The recent history of the chamber will also influence equilibration characteristics; the water stored from one sample being carried over to the next. Cleaning with water may not be advisable for the same reasons.

Errors in porometers, arising from water uptake by surfaces, have also been acknowledged. Perspex walls are said to be responsible for drift phenomena (Morrow and Slatyer, 1971) and polypropylene is recommended by Stigter et al. (1973) on the basis of trials with instruments made of several materials. Gander and Tanner

(1976) studied water uptake by the walls and sensor materials of porometers exposed to much lower values of humidity than in the present study. They found that acrylic plastic was particularly unsuitable, though acceptable if waxed. Stainless steel was preferred over brass because it does not corrode. The magnitudes of water uptake in their study are in broad agreement with those we have found. Attention has been given to the rubber sealing ring in the chambers of diffusion porometers (Stiles, 1970; Hack, 1980). Hack (1980) showed that water retention by this ring could be a serious source of error in the measurement of leaf diffusive resistance. However, the rubber in such sealing rings is usually in the form of foam, in which the water retention properties are exacerbated by the system of interconnected pores.

We conclude that water uptake by wall materials in porometers, although not such a serious problem as in psychrometers, nevertheless deserves careful consideration, and tests on specific materials ought to be made before actual construction is undertaken.

Although a comprehensive list of materials is outwith the scope of this investigation, these results demonstrate the importance of the characteristics of water uptake by surfaces employed as chamber wall materials.

## REFERENCES

- BARRIE, J.A., and PLATT, B. (1963). The diffusion and clustering of water vapour in polymers. *Polymer*, 4, 303-313.
- BARRS, H.D., and SLATYER, R.O. (1965). Experience with three vapour methods for measuring water potential in plants. *Unesco Arid Zone Research*, 25, 369-383.
- GANDAR, P.W., and TANNER, C.B. (1976). Water vapour sorption by the walls and sensor of stomatal diffusion porometers. *Agronomy Journal*, 68, 245-249.
- HACK, H.R.B. (1980). The uptake and release of water vapour by the foam seal of a diffusion porometer as a source of bias. *Plant, Cell and Environment*, 3, 53-57.
- LAMBERT, J.R., and SCHILBGAARDE, J. van. (1965). A method of determining the water potential of intact plants. *Soil Science*, 100, 1-9.
- MILLAR, B.D. (1971a). Improved thermocouple psychrometer for the measurement of plant and soil water potential. I. Thermocouple psychrometry and an improved instrument design. *Journal of Experimental Botany*, 22, No. 73, 875-890.
- MILLAR, B.D. (1971b). Idem. II. Operation and Calibration. *Journal of Experimental Botany*, 22, No. 73, 891-905.
- MILLAR, B.D. (1974) Idem. III. Equilibration. *Journal of Experimental Botany*, 25, No. 89, 1070-1084.

- MORROW, P.A., and SLATYER, R.O. (1971). Leaf resistance measurements with diffusion porometers: precautions in calibration and use. *Agricultural Meteorology*, 8, 223-233.
- PECK, A.J. (1969). Theory of the Spanner psychrometer. II. Sample effects and equilibration. *Agricultural Meteorology*, 6, 111-124.
- RAWLINS, S.L. (1966). Theory for thermocouple psychrometers used to measure water potential in soil and plant samples. *Agricultural Meteorology*, 3, 293-310.
- SHEPHERD, W. (1973). Moisture absorption by some instrument materials. *The Review of Scientific Instruments*, 44, 234.
- SPANNER, D.C. (1951). The Peltier effect and its use in the measurement of suction pressure. *Journal of Experimental Botany*, 2, 145-168.
- STIGTER, C.J., BIRNIE, J., and LAMMERS, B. (1973). Leaf diffusion resistance to water vapour and its direct measurement. II. Design, calibration and pertinent theory of an improved leaf diffusion resistance meter. *Mededelingen van de Landbouwhogeschool te Wageningen*, 73, No. 15, 1-55.
- STILES, W. (1970). A diffusive resistance porometer for field use. I. Construction. *Journal of Applied Ecology*, 7, 617-622.

WEAST, R.C. (Ed.), (1971). Handbook of Chemistry and Physics. The Chemical Rubber Company, Cleveland, Ohio.

WIEBE, H.H., CAMPBELL, G.S., GARDNER, W.H., RAWLINS, S.L., CARY, J.W., and BROWN, R.W. (1971). Measurements of plant and soil water status. Bulletin 484, Utah Agricultural Experiment Station, Logan, 71p.

## ACKNOWLEDGEMENTS

Scanning electron micrographs were made by Dr. Christopher Jeffree, Botany Department, Edinburgh University. Electroplating was by courtesy of Precision Machining Ltd., Dalkeith, Scotland. O-rings were supplied by James Walker and Company Ltd., Lion Works, Woking, Surrey, England. We thank our colleagues in this Department for valuable suggestions made in the course of this work. The experiments were carried out during the tenure of a Research Grant from the Natural Environmental Research Council.



# APPENDIX C.

```

C      FORTRAN PROGRAM "PENITEITH"
C      PENHAM MONTEITH EQUATION
C      DIMENSION SAT(40),UOUT(50)
C      DATA FILE COMPRISING RATE OF CHANGE OF S.V.P. WITH TEMPERATURE
DATA SAT/0.48,0.51,0.54,0.57,0.61,0.65,0.69,0.73,
Z 0.78,0.83,0.88,0.93,0.98,1.04,1.1,1.17,1.23,1.3,
Z 1.37,1.45,1.53,1.62,1.7,1.79,1.89,1.99,2.1,2.21,2.32,
Z 2.44,2.51,2.69, 2.83,2.97,3.12,3.27,3.43,3.57,3.76,3.94/
ROCEEP=1.2*1010
C      UNITS: T IN CELSIUS, RN IN W H-2, VPD IN HB,
C      RA AND RS S CM-1
T=20
V=0.151
D=0.24
ILINE=0
DOSIRN=1,7
RN=FLOAT(IRN-1)*100
DOSIVPD=1,16,3
VPD=FLOAT(IPVD)
DOSIRS=3,11,2
RS=FLOAT(IRS*100)
DOSIDD=1,51,10
DD=FLOAT(IDD)
DD=DD/10
DD2I=1,50
U=FLOAT(I)*10
G=(0.66*(D**.67)*(U**.5))/((DD**.5)*(V**.17))
TG=(.03*(D**.67)*(U**.8))/((DD**.2)*(V**.47))
RA=1/G*100
TR=1/TG*100
IT=IFIX(T)
RAH=RA*1.08/2

C      TOP LINE OF EQUATION
A=(SAT(IT)*RN)+(ROCEEP*(VPD/RAH))
C      BOTTOM LINE OF EQUATION
B=SAT(IT)+(0.66*((RA+RS)/RAH))
C=A/B
C      UNITS KG H-2 S-1
E=C/2453590
C      UNITS MG CM-2 H-1
EMIKE=E*100*60*60
UOUT(I)=EMIKE
C      UNITS MM H-1
EMM=E*60*60
2  CONTINUE
ILINE=ILINE+1
IF(IILINE.EQ.61) IILINE=1
IF(IILINE.EQ.1) WRITE(6,101)
WRITE(6,100) DD, RN, VPD, RS, (UOUT(J), J=1,5), (UOUT(10)),
*UOUT(20), UOUT(30), UOUT(40), UOUT(50)
5  CONTINUE
100  FORMAT(' ',F3.1,F7.1,F6.1,F9.1,F10.2,F8.2)
101  FORMAT('1', ' D RN VPD RS ',
*'EVAP. (MG CM-2 H-1) AT THESE DIFFERENT WIND SPEEDS (M S-1):'
*' / CM W H-2 HB S H-1 0.1 0.2 0.3 0.4
* 0.5 1.0 2.0 3.0 4.0 5.0')
STOP
END

```

## APPENDIX D. Radiation Environment of the Wind Tunnel

The following appendix contains a description of the geometrical distribution of radiation fluxes in the controlled environment wind tunnel used in the preceding experiments.

A study of this nature was prompted by a consideration of the distribution of leaf attitudes or angles, relative to horizontal, in the species tested. It was realized that the original approach to the measurement of  $R_n$  was probably in error, since the horizontal vantage, above the canopy, of the net radiometer permitted it a view of only a few of the uppermost, generally horizontal leaves. Therefore, the instrument would probably have recorded a maximum value of  $R_n$  which would not have been a true average value of the energy absorbed by all the leaves, since a certain percentage were orientated non-horizontally and others were shaded to varying degrees.

In the following study, a miniature net radiometer (Type ME-1, Swissteco Pty. Ltd., Melbourne) and a solarimeter (Kipp and Zonen, Ltd., Netherlands) were used to measure the incoming fluxes of all-wave and short-wave radiation, respectively. The bottom half of the net radiometer was shielded with a low emissivity foil covering - thus the upper surface of the radiometer represented that of a leaf. The instruments were

mounted at plant height (about 25 cm above the floor) and rotated in 30 steps in at least two planes of rotation. This was repeated at two different wind speeds corresponding to the upper and lower limits of wind experienced by the test species. Thus, the general spectrum of leaf orientations was represented and estimates of incoming radiation to both sides of the leaf were obtained.

The distribution of short-wave radiation in the wind tunnel was predominantly in the visible part of the spectrum (Rees, unpublished) and it has been estimated that leaf tissue absorbs approximately 80% of these wave-lengths (Monteith, 1973). Therefore, the total energy absorbed by both sides of the leaf can be represented as follows:

$$\text{Absorbed energy} = (AW_d - SW_d) + (0.8 \times SW_d) + (AW_u - SW_u) + (0.8 \times SW_u)$$

where  $AW$  = all-wave radiation (as measured by the net radiometer) ( $W\ m^{-2}$ )

$SW$  = short-wave radiation (as measured by the solarimeter) ( $W\ m^{-2}$ )

the subscripts, d and u, denote downward and upward fluxes respectively.

The results of estimating the energy absorbed by

individual leaves at various orientations and at two wind speeds are presented in Fig. D.1. A realistic range of average leaf orientations was chosen, bearing in mind that a certain degree of mutual shading occurred which would tend to lower values of absorbed energy. The limits of the chosen range were between 50 and 75% of the maximum total energy absorbed (i.e. the case of the horizontal leaf). Therefore, the original estimates of  $R_n$  were decreased to encompass this range and the Penman-Monteith calculations of transpiration reported in Chapter 6 (Fig. 6-8) were amended, with due consideration to the more realistic values of net radiation (Fig. 6-8, overlay).

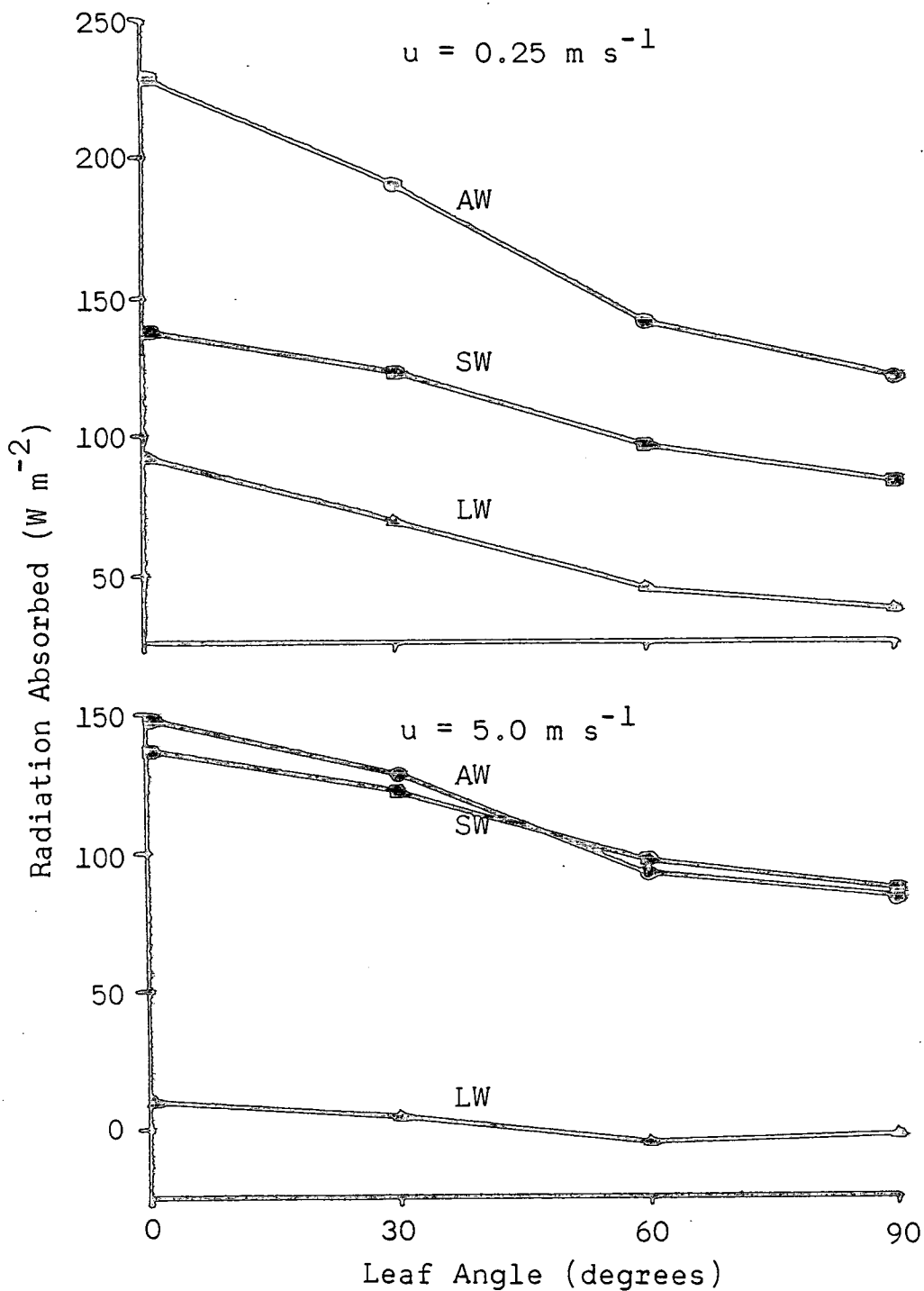


Fig.D.1 Estimates of all-wave (AW), short-wave (SW) and long-wave (LW) radiation absorbed by individual leaves at two wind speeds as a function of leaf angle. Zero degrees represents a horizontal leaf.